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Population and Trophic Dynamics of Striped Bass and Blueback Herring in the Connecticut River

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Case studies of the ramifications of predator management for prey population dynamics can play a valuable role in developing ecosystem fisheries management. My dissertation focuses on the predator-prey interaction between Striped Bass (*Morone saxatilis*), an abundant predatory finfish, and an imperiled prey population of anadromous Blueback Herring (*Alosa aestivalis*). Annual returns of Blueback Herring to the Holyoke Dam on the Connecticut River in southern New England collapsed during the 1980-2000s, coincident with Striped Bass recovery. I studied the abundance and demography of both species in the Connecticut River during 2005-08, measured predation levels, and surveyed the in-river recreational Striped Bass fishery. Herring in 2005-08 were on average younger, smaller, and less likely to be repeat spawners than during the 1960s. These findings suggest elevated mortality operating on adult herring, consistent with other contemporary studies of river herring runs. I estimated that approximately 125,000 Striped Bass were present in the upper 64 km of the river stretch below the Holyoke Dam in spring 2008, and that this predator contingent was capable of consuming 200,000-800,000 adult herring annually. I also estimated that increased in-river recreational Striped Bass harvests might reduce annual predatory losses by 4-10%. I constructed a stage-structured model of the Blueback Herring population spawning above the Holyoke Dam, and used it to a) assess whether Striped Bass predation could explain the collapse of the herring run to the Holyoke Dam, and b) whether reductions in adult herring mortality

effected through increased Striped Bass harvest could substantially improve recovery prospects. Model simulations suggested that Striped Bass predation made a substantial contribution to the collapse of the Holyoke herring run: over 50% of model simulations predicted a run crash, and metrics of population resilience and reproductive potential were greatly reduced in the presence of Striped Bass predation. Increased in-river harvests of Striped Bass offer potential to conserve Blueback Herring under some scenarios; however, the requisite harvest levels appear improbable given the observed intensity of the fishery. This study will inform future efforts to conserve river herring and manage Striped Bass populations, and illustrates the trade-offs inherent to ecosystem-based management.

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Table of Contents

Chapter 1

Introduction

Since the field's inception, ecologists have debated the mechanisms that regulate population size and community organization (Kingsolver and Paine 1991). Predator-prey interactions motivated some of the earliest ecological investigations (Elton 1933; Elton and Nicholson 1942; Lotka 1925; Volterra 1926), yet early ecologists focused primarily on mechanisms related to resource limitation (Lack 1954; Nicholson and Bailey 1935) and abiotic factors (Andrewartha and Birch 1954). An important exception was the text *Animal Ecology* (Elton 1927), in which Elton placed emphasis on the "food chain" as both an organizational scheme for natural communities and a prism through which to view an organism's functional role or "niche" (Kingsland 1991). In so doing, he encouraged emphasis on the feeding habits of animals and the connections that these habits implied. Lindeman expanded on Elton's work by marrying physiological ecology to the food web (Lindeman 1942). Lindeman organized the biotic community into "trophic levels" composed of groups of organisms with similar feeding habits. He then demonstrated how the flow of energy and nutrients across these trophic levels could regulate the structure of natural communities. Lindeman's concept of trophic dynamics in many ways crystallized the understanding that the abiotic and biotic components of the environment were linked and should be studied as a unified "ecosystem" (Kingsland 1991).

Trophic dynamics became a mature paradigm with the publication of Hairston et al. (1960), in which the authors (hereafter referred to as "HSS") proposed a simple yet powerful hypothesis: that the mechanisms of population regulation differ by trophic level (Kingsolver and Paine 1991). HSS observed that in most terrestrial communities the landscape is dominated by green plants, a pattern they attributed to the inability of herbivores to deplete their forage base. Plant populations must therefore be regulated through resource limitation and resultant competition. Conversely, herbivore populations must be regulated by their predators, whose populations are in turn regulated by resource (prey) limitation. HSS thus proposed an expanded framework in which resource limitation, competition, and predation all played important and complementary roles in determining the structure of natural communities.

Despite the controversy it immediately caused (Ehrlich and Birch 1967; Murdoch 1966; Slobodkin et al. 1967), the trophic-dynamic paradigm proposed by HSS demonstrated great utility as a theoretical framework for study of ecological processes. Theoretical ecologists used mathematical models to describe how predators could regulate prey populations (Rosenzweig and MacArthur 1963), and how trophic interaction could produce the types of oscillatory population cycles observed in many natural systems (May 1972). Landmark experimental studies by Holling (1959a; 1959b) linked predator foraging behaviors to their capacity for regulation of prey populations. Empirical evidence also began to accumulate for predation as a strong organizing force in natural communities, much of which came from studies in aquatic (Brooks and Dodson 1965; Hrbacek 1958; Kitchell et al. 1979) and marine (Dodson 1979; Estes and Palmisano 1974; Power and Gregoire 1978) ecosystems. In particular, experimental manipulations of predator populations in marine inter-tidal communities provided clear evidence for the importance of predation (Birkeland 1974; Menge 1976; Paine 1966; Paine 1974). These experiments also demonstrated that predation was critical in determining the outcome of competitive interactions at lower trophic levels (Paine 1980), a finding that supported the inclusive framework proposed by HSS.

Today predation is widely considered to be a primary organizing force in nature on par with resource limitation and competition (Fretwell 1987). The maturation of the trophic-dynamic paradigm has moved population and community ecology towards more integrative theoretical frameworks that recognize the complementary roles of "bottom-up" (i.e. related to resource limitation) and "top-down" (i.e. related to predation) forces (Oksanen and Ericson 1987). Theoretical ecologists have expanded the predator-prey models of Rosenzweig and MacArthur (1963) to incorporate the bottom-up influence of primary productivity and accommodate higher-order trophic pyramids (Fretwell 1977; Oksanen et al. 1981; Rosenzweig 1973). Empirical examples of the importance of top-down control in freshwater and marine systems have also continued to accumulate (Baxter et al. 2004; Daskalov 2002; Estes et al. 2004; Frank et al. 2005; Frank et al. 2007; Pelicice et al. 2015; Simberloff et al. 2013; Springer et al. 2003; Vitule et al. 2009).

Given that the fields of ecology and fisheries science grew in a mutualistic fashion throughout the 20th century (Nielsen 1999), it is not surprising that predation has also been of central interest to fisheries managers. Trophic dynamics have played a particularly important role in the maturation of freshwater fisheries management. An early example was the work of Swingle (1950), who, through a series of experimental manipulations of fish populations in small freshwater ponds, demonstrated that manipulating ratios of predator to prey abundances was important to maintaining "balanced" fish populations that could sustain sufficient harvest rates to provide quality recreational fishing. Swingle's concept of balanced fish populations remains highly influential in management of freshwater impoundments (Anderson and Weithman 1978; Flickinger et al. 1999; Ploskey and Jenkins 1982). Empirical evidence for trophic cascades in freshwater lakes (Carpenter and Kitchell 1988; Carpenter et al. 1985) also led fisheries managers to recognize the potential for manipulation of physical and chemical habitat via manipulation of fish populations. Initiation of trophic cascades via large-scale removals of zooplanktivorous and benthivorous fish, a practice commonly referred to as "biomanipulation", has become an important tool for remediating lakes plagued by poor water quality (Horppila et al. 1998; Kairesalo et al. 1999). Quantification of predator-prey relationships has also been central to the design of freshwater fish stocking programs (Baldwin et al. 2003; Christensen and Moore 2010; Yule et al. 2000), projecting impacts of invasive species on native freshwater fishes (Love and Newhard 2012; Walrath et al. 2015), and recovery planning for endangered or threatened species (Krueger et al. 2013; Naughton et al. 2004; Tabor et al. 2007). Food habit studies of freshwater fishes have also been central to the development of standard analytical methods for quantifying fish consumption (Elliot 1991; Kitchell et al. 1977; Trudel et al. 2000).

Marine fisheries management has been slower to formally incorporate trophic dynamics. Studies of marine systems were central to the development of ecological understanding of predator-prey dynamics (e.g. Connell 1961; Estes and Palmisano 1974; Paine 1969), but marine fisheries management through much of the twentieth century reflected a viewpoint that predation was insignificant relative to fishery removals (Sissenwine and Daan 1991). Marine fisheries were therefore managed using "single

species" models which assumed target species abundances were primarily a function of fishery removals and environmental stochasticity (Christensen 1996). Subsequently, widespread fishery collapses during the 1960-80s prompted a general re-consideration of prevailing marine fishery management practices (Whipple et al. 2000). Among other corrective measures, marine fishery managers began to give greater consideration to the potential importance of interactions between species, particularly predator-prey relationships (Bax 1998; May et al. 1979; Vetter 1988). Recent years have seen a proliferation of case studies concerning the potential importance of predation to managed fish species and the development of quantitative models that explicitly account for predation (Bundy and Fanning 2005; He et al. 2015; Lacroix 2014; Link et al. 2009; Link and Idoine 2009; Mohn and Bowen 1996; Moustahfid et al. 2009; Punt and Butterworth 1995; Temming and Hufnagl 2015). This heightened interest in measuring and modeling predator-prey interactions reflects a growing consensus for the adoption of an "ecosystem approach" to fishery management (EAFM) in which ecological considerations are given greater primacy in management planning (Fogarty 2014).

The call for greater attention to ecological principles in fisheries management has been pervasive in the fisheries science field for at least two decades (e.g. see Mooney 1998), yet implementation of management strategies that explicitly account for important ecological interactions is not yet commonplace (Pitcher et al. 2009). One stumbling block is the perceived intractability of constructing and parameterizing complex models that account for all the relevant biological interactions within an ecosystem. However, relatively simple models with modest data requirements can offer valuable insight into managing a group of inter-related species, are more tractable for management agencies faced with limited budgets, offer greater transparency to stakeholders, and avoid problems (e.g. "overfitting") characteristic of more complex models (Fogarty 2014). Therefore, when faced with a situation in which, for instance, the management of a predator species is perceived to have significant ramifications for prey population dynamics, quantification of the predator-prey interaction and incorporation of that knowledge into management planning represents a valuable first step towards ecologically-minded management.

In this dissertation, I address the question of how past and future management of Striped Bass (*Morone saxatilis*) fisheries impact a population of anadromous Blueback Herring (*Alosa aestivalis*). Blueback Herring and closely-related Alewife (*A. pseudoharengus;* the two species in aggregate are often referred to as "river herring") have experienced dramatic declines throughout much of their range along the Atlantic coast of North America (ASMFC 2012). One prominent hypothesis concerning the mechanism for these declines centers on Striped Bass, a large predatory finfish sympatric with river herring that has recently recovered from historically low abundances and may therefore be exerting increased top-down control on prey resources (Grout 2006; Hartman and Brandt 1995; Hartman and Margraf 2003; Heimbuch 2008; Savoy and Crecco 2004; Uphoff 2003). The recovery of Atlantic Striped Bass stocks is one of the great fisheries management success stories of the 20th century (Richards and Rago 1999) – yet the predatory demands of a robust Striped Bass population were not considered in the Striped Bass management process that produced recovery. In this dissertation, I assess whether increases in coastal Striped Bass stocks achieved in part through fisheries management decisions played a substantial role in the decline of a prey population, and investigate whether alternative management of a recreational fishery for Striped Bass might improve prey recovery prospects.

Elevated mortality rates are a logical explanatory hypothesis for population declines; what is usually most important from both an ecological and management perspective is determining the source and selectivity of that mortality. Size- or age-dependent mortality often leaves a characteristic signature in the form of temporal shifts in demography and life history. For instance, mortality operating on larger, older animals within a population will reduce the abundance of older age classes and favor the rapid evolution of earlier maturation at smaller sizes (Conover et al. 2005; Reznick and Endler 1982; Reznick and Ghalambor 2005; Ricker 1981; Rodd and Reznick 1997). With respect to declining river herring populations, reduction of older individuals, earlier age- and size-at maturation, and loss of repeat spawners are all predicted by the Striped Bass hypothesis (Davis and Schultz 2009). In Chapter 2, I provide evidence that such shifts have occurred in the Connecticut River Blueback Herring population,

and also provide previously-unavailable information on demography as well as spatial and temporal migratory dynamics of this important population.

Fishery closures may fail to produce significant recovery of depleted fish populations (Dempson et al. 2004; Hutchings and Reynolds 2004). Factors potentially contributing to recovery failure include maladaptive changes in life history traits (Hutchings 2005; Walsh et al. 2006), release of interspecific competitors (Link and Garrison 2002; Swain and Sinclair 2000), and intensified predation (Bailey and Houde 1989; Walters and Korman 1999). Predation is of particular concern to fisheries managers as depensation (a decline in per-capita population growth rate) can occur when predators drive prey to low abundances (Frank and Brickman 2000; Shelton and Healey 1999). Populations subject to depensation often shift into domains of population behavior that are unresponsive to management, and can even decline towards extinction (Hilborn and Walters 1992; Spencer 1997; Walters and Kitchell 2001).

If a threatened prey species fails to respond to traditional management measures (e.g. fishery restrictions or closures, habitat restoration), regulations that encourage increased predator harvests may reduce natural mortality of threatened prey species and help effect population recovery (Yodzis 2001). River herring fisheries have been closed in the Southern New England for over a decade, but the Blueback Herring population in the Connecticut River has been slow to recover. Given that there is a popular directed recreational fishery for Striped Bass in the Connecticut River (Davis et al. 2011), adoption of regulations that increase Striped Bass harvest opportunities may ameliorate predation mortality and improve prospects for Blueback Herring recovery. A necessary prerequisite for such a management strategy is quantitative assessment of the predator-prey interaction. In Chapter 3, I use information on striped bass abundance, size structure, and food habits to estimate annual population-level consumption of Blueback Herring by Striped Bass in a portion of the Connecticut River during the spring migration season. I then use data on the recreational fishery for Striped Bass in that section of the Connecticut River to assess whether alternative Striped Bass harvest regulations might significantly decrease annual Striped Bass consumption of Blueback Herring.

In Chapter 4, I synthesize information from Chapter 2 and 3, along with other available information on Blueback Herring and Striped Bass biology, in a structured population model with the goal of assessing a) the plausibility that Striped Bass consumption played a substantial role in declines of Blueback Herring annual run size at the Holyoke Dam on the Connecticut River during the 1990-2000s, and b) the potential increases in Holyoke herring run size that could be achieved via increased in-river recreational harvests of Striped Bass. I parameterize a stage-structured population model (Morris and Doak 2002) for the "above-Holyoke" Blueback Herring population in the Connecticut River (i.e. considering the segment of the Connecticut River population spawning above Holyoke Dam as a distinct population), using Blueback Herring demographic data reported in Chapter 2 and from other studies. I then extend this model to incorporate dynamic estimates of mature herring mortality arising from in-river Striped Bass predation. I use this extended model to project the trajectory of the above-Holyoke herring population during the 1980-2000s, incorporating estimated rates of annual Striped Bass predation, to assess the plausibility that in-river Striped Bass predation produced the observed collapse in the above-Holyoke herring population. Finally, I incorporate estimates of annual reductions in Striped Bass predation potentially achieved through alternative management of the in-river fishery (Chapter 3), and assess whether alternative in-river Striped Bass management scenarios could substantially improve prospects for recovery of the above-Holyoke herring population from its current state of depressed abundance.

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Chapter 2

Demography of anadromous Blueback Herring in the Connecticut River

Abstract

Recent range-wide declines have highlighted the need for information on the demographic composition of populations of anadromous river herring (Alewives *Alosa pseudoharengus* and Blueback Herring *A. aestivalis*). Here we report demographic data for the Blueback Herring run in the Connecticut River, the largest river in New England and a system from which contemporary river herring demographic data were not previously available. We collected Blueback Herring in a stretch of the Connecticut River via boat electrofishing during the spring migration seasons of 2005-07, and assessed relative abundance, size and age structure, spawning history, and sex ratio. Significant inter-annual variation was evident during study years: Blueback Herring were less abundant in 2005 than in 2006-07, but were generally older, larger, larger-at-age and more likely to be repeat spawners. However, despite inter-annual variation, herring collected during our study were on average much smaller, younger, and less likely to be repeat spawners than those collected during a similar study in the 1960s, suggesting that in recent decades this population has experienced truncations of size and age structure and loss of repeat spawners similar to those reported for other river herring populations. There were also significant within-year spatial and temporal patterns in demography. Mean relative abundance and length were lowest and sex ratio was skewed towards male fish in the upstream portion of our study area; early migrants to our study area were typically larger and more likely to be female. These findings suggest that the portion of the Connecticut River Blueback Herring run migrating to the Holyoke Dam fish passage facility, the upper terminus of our study area at which this run has been enumerated annually since the 1970s, may not be representative of the abundance and demography in the more downstream areas, and that earlier migrants to the Connecticut River may make a disproportionately high contribution to annual reproductive output.

Introduction

Better understanding of the demography of imperiled populations can aid effective conservation planning. For instance, demographic modeling of threatened loggerhead sea turtle (*Caretta caretta*) populations in U.S. waters revealed that improving adult turtle survivorship was more likely to produce population increases than the prevailing strategy of protecting nestlings, leading to the current regulatory emphasis on reducing incidental adult turtle bycatch in offshore trawl fisheries (Crouse et al. 1987; Crowder et al. 1994). Demographic modeling that incorporated updated estimates of northern spotted owl (*Strix occidentalis caurina*) longevity, survivorship, and dispersal rates demonstrated the inadequacy of prevailing management practices for conserving this imperiled species in the Pacific Northwest region of the US (Lande 1988). Time series of demographic data collected prior to and during the 1980-90s population crash of the Northern Stock of Atlantic Cod (*Gadus morhua*) provided evidence that intense fishing pressure had caused rapid evolution of earlier maturation and smaller body size-at-age, a finding that helped fishery managers understand the slow pace of population recovery following a fishery moratorium (Olsen et al. 2004). A common thread running through these and other examples is that more effective management planning is predicated on collection and utilization of demographic data.

A paucity of demographic data is a primary obstacle to addressing recent range-wide declines in abundance of anadromous river herring (Alewives *Alosa pseudoharengus* and Blueback Herring *A. aestivalis*) along the east coast of North America (ASMFC 2012; Limburg and Waldman 2009). In the early 20th century, river herring were abundant enough to support significant commercial fisheries throughout much of their range, but the combined effects of overfishing, habitat loss, and declining water quality caused widespread population declines and attendant reductions in commercial landings by mid-century (Schmidt et al. 2003). Increased attention to restoring the connectivity and quality of riverine habitats along the eastern seaboard during the second half of the 20th century allowed partial recovery of some populations (Gephard and McMenemy 2004). However, beginning in the 1990s, sharp declines in "run size", or numbers of adult fish participating in vernal spawning migrations, were observed in many systems, prompting regional fishery closures, revision of State and Federal management plans, listing of

river herring in the US by the National Oceanic and Atmospheric Administration (NOAA) as a "Species of Special Concern", and a petitioning of NOAA by the Natural Resources Defense Council to list river herring as a "Threatened Species" in the U.S. pursuant to the Federal Endangered Species Act (ASMFC 2012; NOAA 2015). It is now widely accepted within the fisheries management community that river herring populations range-wide are in crisis (Hasselman and Limburg 2012).

Biological monitoring of river herring has historically been assigned lower priority than monitoring of other more commercially-significant species (Hasselman and Limburg 2012; Limburg and Waldman 2009). As such, the status of many populations remains undocumented (Schmidt et al. 2003). For populations that have been subject to long-term monitoring efforts, available data are mostly limited to time series of annual run sizes – information of value for assessing coarse temporal or spatial trends in abundance but of limited utility for predictive modeling of future population states (Gibson and Myers 2003) or quantitative hypothesis testing concerning causative mechanisms for population declines (Hilborn and Mangel 1997). The limited demographic data available suggests that mean size and age of spawners as well as the incidence of repeat spawning has declined in some populations (ASMFC 2012; Davis and Schultz 2009; Palkovacs et al. 2014; Schmidt et al. 2003). Detailed demographic information, particularly from systems for which such data have not previously been reported, will be valuable in inferring the generality of this trend. Demographic data are also required to assess the appropriateness of current management initiatives (ASMFC 2012; Cournane et al. 2013). Contemporary demographic data will be particularly valuable for systems in which historic data (i.e. prior to recent population crashes) exists and inferences can therefore be drawn about causative mechanisms for declines.

Annual time series of demographic data are a necessary building block for effective conservation and are therefore rightly a primary focus of the response to the river herring crisis; however, information on within-river or within-year temporal and spatial structuring of runs may also inform management. For instance, restoration of access to upstream spawning habitat has been and continues to be a central focus of contemporary diadromous fisheries restoration. In an era of increasing budgetary challenges, better understanding of spawning site selection and the relative importance of various habitats will inform

prioritization of fish passage and dam removal projects (Harris and Hightower 2010; Harris and Hightower 2012). Aggregations of river herring within unimpeded sections of river may indicate the location of important spawning habitats, the attributes of which can aid in identification of similar high value habitats above barriers to fish passage in other systems. Spatial structuring of river herring runs can also provide insight into the effectiveness of the common strategy of fixed-point monitoring at fishways. Fish passage facilities provide convenient locations for enumeration and collection of migrating fish, and the majority of available data for river herring are generated at such locations (ASMFC 2012). It is unclear whether this practice provides an unbiased sample of population structure; more extensive spatial sampling within systems that have historically been monitored by fishway sampling may elucidate inherent biases. Temporal dynamics of spawning migrations may also provide insights valuable for management. For instance, larger females of some fish species make outsize contributions to population recruitment (Hixon et al. 2014; LaPlante and Schultz 2007). Larger females of some migratory species arrive at spawning sites earlier than smaller females (Schultz et al. 1991), suggesting that management actions designed to protect early migrants may be particularly effective at conserving imperiled populations. Understanding spatial and temporal run dynamics may also be important when considering hypothetical agents of decline that have a distinctive temporal or spatial signature, such as a predator that is not uniformly distributed within a riverine system or is only present on the spawning grounds during a portion of the migration season.

More intensive study of river herring runs in Southern New England may be particularly valuable as populations within this region have experienced some of the most severe declines observed range-wide (Palkovacs et al. 2014), and may also be particularly vulnerable to stressors such as marine bycatch and predation (Hasselman et al. 2016; Savoy and Crecco 2004). The Blueback Herring run in the Connecticut River, the largest river in Southern New England, is an oft-cited exemplar of the current river herring crisis. Blueback Herring run size, enumerated annually since 1969 at the fish passage facility at Holyoke Dam in Holyoke, Massachusetts, has declined from a peak of 630,000 fish in 1985 to an average of approx. 250 fish during 2004-14 (USFWS 2015). Outside of annual enumeration of Blueback Herring

passing the Holyoke Dam, the run in the Connecticut River is relatively unstudied. A single previous study assessed size structure in a Connecticut River tributary in 1967 (Loesch 1969). Further, little is known about the spatial and temporal characteristics of upstream migration by Blueback Herring over the course of the spawning season in the Connecticut River. It is unclear whether the annual monitoring program conducted at Holyoke, situated 140 km above the mouth of the river, provides an accurate estimate of run size and composition.

We conducted a demographic study of the Blueback Herring population in the Connecticut River with the goals of providing previously unavailable data for an important river herring run, assessing the efficacy of a monitoring program based on fixed-point sampling at a fishway, and providing information on within-river and within-season demographic patterns that may aid in formulating management strategies. The specific objectives of our study were to a) characterize demography (age and size structure, length-at-age, spawning history, and age-at-maturity) of the Blueback Herring run to the Connecticut River during 2005-07; b) assess decadal temporal trends in demography via comparisons to historical demographic data from the 1960s for this population and adjacent populations; c) assess within-river spatial structuring of the run with respect to relative abundance, length, and sex ratio; and d) assess within-season temporal trends in relative abundance, length, and sex ratio within our study area. With respect to objectives a) and b), given the observed pattern of reductions in mean length, age, and repeat spawning frequency in other river herring populations, we predicted that the Connecticut River Blueback Herring run would display similar decadal shifts in demography and would therefore consist primarily of small, young fish that had not spawned previously. With respect to objective c), absent *a priori* information on the distribution or relative importance of various spawning habitats within our study area, we made no predictions concerning spatial patterns of relative abundance; however, we did predict, given the presumed greater swimming capabilities of larger fish, and previous observations that female river herring typically recruit to spawning runs at older ages and larger sizes than males (Loesch 1987), that mean herring length and proportion of females would be highest in our upstream sample sites. With respect to objective d), given evidence from other river herring populations of earlier arrival of males to

spawning sites as well as seasonal declines in mean herring length (Cooper 1961; Havey 1961; Kissil 1974; Libby 1981; Rideout 1974), we predicted that sex ratios would be skewed towards males during the early portion of the migration season and that mean length would decline over the season.

Methods

Study area and field sampling

We collected Blueback Herring (hereafter referred to simply as "herring") by night-time boat electrofishing in the Connecticut River segment between Wethersfield, Connecticut (near the head of tide) and the dam at Holyoke, Massachusetts (a 64 km stretch hereafter referred to as the "study area", see Fig. 1) during spring 2005-07. We selected this river stretch because it is immediately downstream of the Holyoke dam, and its relatively narrow and shallow geomorphology facilitated boat electrofishing. In 2005, we used a 5.5 m electrofishing boat equipped with a Coffelt VVP and a 1-meter "Wisconsin Ring" style electrode. In 2006-07, we used a Smith Root Model SR-18 electrofishing boat equipped with a 5.0 GPP electrofisher and two SAA-6 electrode arrays. During the spring of each study year, sampling was planned to begin as soon as river stage permitted access and cease once herring catch rates became consistently low and/or river stage became too low for safe navigation. We sampled fixed transects located parallel to the shoreline in near-shore, shallow habitat (≤2 m depth) at the same five sites (Fig.1) weekly, river conditions and equipment permitting.

The duration of the sampling season and the number of sampling nights completed varied among study years. In 2005, a total of 23 sampling nights was completed between May 10 and June 15. In 2006, 30 sample nights were completed between April 27th and June 29th. In 2007, sampling was initiated on May 6th and discontinued after June 13th, during which time a total of 25 sampling nights was completed. In 2006 and 2007, there were some departures from the planned temporal frequency (one sample per calendar week) of sampling at each standard sample site, including four short weeks (two sample nights or fewer) during 2006 due to flooding events and equipment failures (May 13-27, June 3-17), and discontinuation of sampling at Enfield in 2007 after May 16 (two sample nights total in 2007). Samples

obtained during short weeks in 2006, as well as samples collected at Enfield in 2007, were included in analyses of relative abundance, size and age structure, and spawning history but were not used in analyses of within-river and within-season trends in demography.

Relative abundance and size structure

All herring captured were counted and measured for total length (TL). Catch-per-hour (CPH) for each sample night was estimated as the number of herring caught per second of electrofishing "on" time.

The proportion ($\hat{P}_i$) of herring in each 5-mm size class in each year was estimated as:

$$\hat{P}_i = \left(\sum_j p_{i,j} w_j \right) \quad (1)$$

where: $p_{i,j}$ = proportion of herring in size class *i* at site *j;* and w_j = weighting factor for site *j* calculated as:

$$w_j = \frac{\overline{E}_j}{\sum_j \overline{E}_j} \quad (2)$$

where: $\overline{E}_j$ = mean electrofishing CPH of herring at site *j* (across all electrofishing samples collected in the year of interest). Weighting factors were used to correct for potential biases introduced by unequal numbers of sampling nights among sites in each study year. Once the corrected proportions of herring in each 5-mm size class in each year were estimated from equation 1, the frequency of herring in each size class in each year was estimated as the product of these proportions and the total number of herring collected in that year; these frequencies were then standardized to total electrofishing effort in each year to estimate CPH by size class.

Age structure and spawning history

On each sample night, a maximum of up to five herring per 5 mm size class were euthanized and retained as sub-samples for determination of species, sex, age and spawning history. Subsampled herring were placed on ice and subsequently dissected within 24 h. Species determinations were made based on peritoneal color (Loesch 1987). A small number (3% or less) of Alewives were identified in the lethal

sub-sample in each study year; these herring were eliminated from further analyses. Sex determinations were made based on examination of the gonads. Scale samples and sagittal otoliths were also collected from all lethally subsampled herring. Scales were taken from the area above the lateral line and anterior to the dorsal fin (Hattala 1999).

A stratified random sample (*n*=maximum of 10 from each year/sex/cm TL stratum) of subsampled herring was selected for analysis of age and spawning history (*n*=439). Otoliths are widely considered to be more reliable estimators of age than scales for most fish species, especially for older fish (Maceina et al. 2007). In a previous reader trial, otoliths and scales provided similar levels of inter-reader precision, but otoliths tended to provide older age estimates for individual herring (Davis et al. 2009). Accordingly, we used otoliths to estimate age. Because readers consistently reported difficulties in interpreting the edge of otoliths from larger herring, we designated all individuals producing age estimates >5 years as "age 6+". A single reader estimated the age of all herring selected for age and spawning history analysis; a second reader subsequently screened a portion (*n*=245) of these otoliths to assess inter-reader agreement. The two readers agreed on age for 82% (*n*=200) of the otoliths, and disagreed by more than one year in <2% (*n*=4). Given this high level of agreement, we used the initial reader's age estimates for age assignment. After age assignment was completed for all otoliths, log-length was regressed on estimated age for each sex in each year; all otoliths producing age estimates that fell outside the 95% prediction interval for each regression (*n*=17, or 3%) were deemed outliers and eliminated from further analyses. A single reader estimated spawning history using scales (otoliths do not provide information on spawning history) for a portion (*n*=322) of the herring selected for age and spawning history analysis.

Sex and age composition of each cm size class for each year was determined from dissection and otolith analysis. The number of herring of sex *a* and age *b* in each year ($\hat{N}_{a,b}$) was then estimated as:

$$\hat{N}_{a,b} = \sum_{i} (\hat{P}_i * N) * (p_{a,i} * p_{b,i}) \qquad (3)$$

where: $\hat{P}_i$ = estimated proportion of herring in cm size class *i* (from equation 1, aggregated from 5 mm to cm size classes); *N*=the total number of herring collected in that year; $p_{a,i}$ = proportion of herring of sex a in size class *i* (from dissection); and $p_{b,i}$ = proportion of herring of age b in size class *i* (from otoliths). The number of herring of sex *a* and spawning history *r* ($\hat{N}_{a,r}$) in each year was then estimated as:

$$\hat{N}_{a,r} = \sum_b \hat{N}_{a,b} * p_{a,b,r} \quad (4)$$

where: $\hat{N}_{a,b}$ = estimated number of herring of sex *a* and age *b* (equation 3; and $p_{a,b,r}$ = proportion of herring of sex *a*, age *b* and spawning history *r* (from scales). Because fish with more than two previous spawns were rare, spawning history was condensed to "0" (i.e. virgin fish), "1", and "2+" previous spawns. Age structures, and therefore spawning histories, were aggregated across sexes as age structures differed significantly (∞=0.05) between sexes in only one year (2005: χ^2=1.1, p=0.77; 2006: χ^2=5.4, p=0.15; 2007: χ^2=75.2, p<0.0001).

Historical, within-river, and within-season trends in demography

We assessed decadal trends in size structure by comparing 2005-07 size structures to those reported for Blueback Herring from a Connecticut River tributary (Roaring Brook in Glastonbury, CT) in 1966 and a tributary of the nearby Thames River (Trading Cove in Montville, CT) in 1967 (Loesch 1969). Marcy (1969) reported age structure and spawning history for a pooled sample of Blueback Herring collected from the Connecticut and Thames Rivers in 1966 and 1967; we used these data as a basis for historical comparisons for our age structure and spawning history data from the Connecticut River.

To assess within-river and within-season trends in demography, we summarized relative abundance (CPH), mean length, and sex ratio of herring by site and calendar week. The number of fish of each sex collected on each sample night was estimated by applying the estimated proportions of each sex in each 10-mm size class ($p_{a,i}$ from equation 3) to the number of fish collected in each 10-mm size class. We used generalized linear models to test for year, site, and week effects on the three variables of interest, assuming appropriate error distributions for each response variable (CPH: negative binomial; mean

length: Gaussian; sex ratio: binomial). Year was treated as a fixed effect, rather than random, as the low number of sample years prevented convergence of mixed models for most analyses.

Results

Relative abundance, size and age structure, and spawning history

Herring abundance increased steadily across study years. Totals of 555, 1,523, and 1,673 herring were collected in 2005-2007, respectively. Relative abundance of herring increased in each study year (2005: mean CPH across all sample nights=48; 2006=66; 2007=80). Size structure varied among study years (Fig. 2). Although the 2005 run was characterized by lower overall relative abundance, larger herring were more prevalent: our sample was composed primarily of fish 245-284 mm TL with a mean size of 265 mm TL. The 2006 and 2007 runs were dominated by smaller fish, being composed primarily of 225-244 mm TL fish in 2006 (mean=244 mm TL) and 240-269 mm TL fish in 2007 (mean=256 mm TL).

Age structure varied among study years. The 2005 run contained a higher percentage of older herring than subsequent years: a majority (56%) of the 2005 run comprised age 5+ fish (Fig. 3). In 2006-07, younger fish dominated the run; the modal age was 3 years in 2006 and 4 years in 2007. Herring of age 3-5 collected in 2005 were also generally larger-at-age than in the two subsequent study years (Fig. 4).

The run in each study year was composed primarily of virgin fish. Incidence of repeat-spawners was highest in 2005 (69% virgin fish, 20% one previous spawn, 11% two or more previous spawns). In both 2006 and 2007, 84% of herring were virgin fish (2006: 9% one previous spawn, 7% two or more previous spawns; 2007: 10% one previous spawn, 6% two or more previous spawns). The modal age of virgin fish was either three (2006) or four (2005 and 2007) in each study year (Fig. 3). However, a non-trivial percentage of fish age 5 or older showed no evidence of previous spawning in each year, particularly in 2005, in which approximately 40% of virgin fish were age 5 or older (Fig. 3).

Historical, within-river, and within-season trends in demography

Herring were younger, smaller (both overall and at-age), and less likely to be repeat spawners in contemporary Connecticut River runs. Herring averaged 288 mm and 300 mm TL in 1967 for male and female herring, respectively, at Roaring Brook, a tributary to the Connecticut River, and 277 mm and 289 mm TL in 1966 at Trading Cove, a tributary of the nearby Thames River. Herring in our study averaged 244-265 mm TL in each study year, representing a potential decline of 8-19% in mean body length when compared to the historic Roaring Brook data. Marcy (1969) reported that Blueback Herring collected from the Connecticut and Thames Rivers in 1966-67 were predominantly older, repeat-spawning fish: approximately 85% of herring were age 5 and older (Fig. 3), fish younger than age 4 were rare, and repeat-spawners composed 82% of the sample. These population structures contrast markedly with those from our study in 2005-07, in which only 26-56% of the sample consisted of fish age 5 and older, fish younger than age 4 were present in appreciable numbers and even comprised the bulk of the run in one year, and repeat spawning frequency was much lower (16-31%). Blueback herring in the Connecticut and Thames Rivers in 1966-67 were also larger-at-age than herring we collected in the Connecticut River in 2005-07 (Fig. 4).

During 2005-07, herring were more abundant and larger in the downstream portion of our study area. Mean CPH at the most downstream sites in our study area (Wethersfield and Farmington River) was generally a magnitude of order higher than at the upstream Enfield and Holyoke sites in each study year (Fig. 5; generalized linear model: year $p=0.04$, site $p<0.0001$, week $p=0.0008$), and herring were consistently smallest at the Holyoke site in each year (general linear model: year $p<0.0001$, site $p=0.0004$, week $p<0.0001$). Female herring were proportionally least abundant at Holyoke in each study year (Fig. 5), although site was not a significant predictor of the sex composition of samples (generalized linear model: year $p=0.003$, site $p=0.96$, week $p=0.05$). Herring were also generally most abundant, largest, and more likely to be female in samples collected early in the season in each year (Fig. 6). In 2005 and 2007, CPH was highest during the early portion of the sampling season and then gradually declined; in 2006, CPH peaked mid-season and then declined (although this result should be interpreted with caution due to

non-inclusion of short weeks in May and June). In each study year, the mean size and proportion of females in the sample was highest in the first week (2005 and 2007) or second week (2006) of the season and then subsequently declined. In 2006, mean length and proportion females was lowest at the end of the sampling season, while in 2005 and 2007 mean length and proportion females declined until late May and then began to increase again.

Discussion

Our study of the Blueback Herring run to the Connecticut River provides previously unavailable demographic data for an important river herring run in the largest river in Southern New England. Herring migrating to our study area in 2005-07 were mostly virgin age 3-5 fish that were 22-27 cm TL. There was significant inter-annual variation during our study years – in particular, herring in 2005 were on average less abundant but older, larger, larger-at-age and more likely to be repeat spawners than herring collected during 2006 and 2007. Size and age structures of the 2006 and 2007 runs showed evidence of a strong 2003 year class (age-3 in 2006, age-4 in 2007) recruiting to the spawning run. Overall, despite evident inter-annual variation, comparison of our contemporary data to data collected during the 1960s demonstrates that the Connecticut River blueback herring population has experienced substantial decadal shifts in demography. Blueback herring sampled in the Connecticut and Thames Rivers during 1966-67 were 8-19% longer, older (85% age 5 or older vs. 26-56% age 5 or older in 2005-07), more likely to be repeat spawners (82% repeat spawners vs. 16-31% in 2005-07), and larger-at-age than the Blueback herring we sampled during 2005-07. Our sampling also revealed significant within-year spatial and temporal patterns in Blueback Herring relative abundance, size, and sex ratio. Blueback herring were consistently most abundant and largest in the downstream portion of our study area, and females were also proportionally more abundant in downstream sample sites. In addition, early migrants to our study stretch were generally larger and more likely to be female.

Demography of contemporary Blueback Herring runs is under-reported relative to Alewive runs, but comparisons of our data to other available contemporary data suggests similar demographic

composition to other Blueback Herring runs in New England. For example, demographic data reported by the New Hampshire Department of Fish and Game for Blueback Herring runs to five New Hampshire rivers during 1994-2010 indicate that runs were dominated by virgin age 3-4 herring 24-28 cm TL (ASMFC 2012). Similarly, data reported by the Massachusetts Division of Marine Fisheries for Blueback Herring runs to six Massachusetts rivers indicates that since 2000, runs have generally been composed of virgin age 3-5 herring with average lengths of 23-24 cm (ASMFC 2012). The general range-wide pattern evident from Blueback Herring runs for which both contemporary data and a basis for historical comparison exists is truncation of age and size structure and loss of repeat spawners (ASMFC 2012; Davis and Schultz 2009; Palkovacs et al. 2014; Schmidt et al. 2003). This finding is troubling as it suggests that the Connecticut River run, like other runs range-wide, is likely in state of decreased viability and lower resilience (Davis and Schultz 2009). Therefore, current management priorities of increasing the number of age classes, abundance of larger fish and incidence of repeat spawning in river herring runs range wide (ASMFC 2012) are certainly also appropriate for the Connecticut River Blueback Herring run.

The substantial inter-annual variation in demography observed among our study years underscores the importance of annual, long-term monitoring. In particular, the 2005 run featured a relatively high proportion of fish age 5 or older, which were also on average larger (both overall and at-age) and more likely to be repeat spawners. Although the 2005 run still featured lower proportions of large, old, repeat-spawning fish than the runs studied in 1966-67, the difference between the 2005 run and the 1966-67 runs was less substantial than between the 2006-07 and historic runs. Within the 2006 and 2007 runs, there was an evident strong 2000 year class, appearing as three year olds in the 2006 run and four year olds in the 2007 run. The inter-annual variation noted in contemporary Blueback Herring runs to the Connecticut River stands in contrast to the findings of our previous study of an Alewife run in the same region (Davis and Schultz 2009), during which the demographic composition of the Alewife run was relatively stable across four study years; further, the comparison of any one of those study years to historic data from the 1960s suggested decadal shifts of similar magnitude. Previous studies of closely-related American Shad (*A. sapidissima*) in the Connecticut River have demonstrated significant variation

in year class strength as a function of riverine conditions during the larval phase of life (Crecco and Savoy 1984; Crecco and Savoy 1987); it is probable that year class strength is similarly variable for Blueback Herring in the Connecticut River, and that variation in year class strength may produce significant inter-annual variation in demographic composition of herring returning to the river to spawn. Such inter-annual variation does not likely account wholly for the difference noted here between contemporary runs and historic runs, but caution should nevertheless be exercised when comparing demographic data from this and other large river systems across years.

Our sampling program provides clear indications that the contingents of Blueback Herring migrating to the Holyoke Dam during 2005-07 were not a representative indicator of abundance or demographic composition of herring in more downstream sites. Electrofishing CPH was consistently a magnitude of order higher in the downstream Wethersfield and Farmington River sites than at Holyoke, and herring were also larger in these downstream sites. Preliminary histological analyses of ovaries dissected from herring collected in downstream sites revealed the presence of post-ovulatory follicles, indicative of previous spawning activity in that season. The higher abundance of herring at our downstream sites may indicate the presence of important spawning habitats in these areas; indeed, it is possible that in their current state of depressed overall abundance, herring are predominantly utilizing habitat in downstream areas rather than undertaking longer upstream migrations that bear a greater energetic cost. It is also possible that Striped Bass (*Morone saxatilis*), a known predator of river herring that has become highly abundant in the upstream portion of our study area in recent decades (Davis et al. 2009; Davis et al. 2012; Savoy and Crecco 2004), play a role in depressed herring abundance in upstream areas, either by preying heavily on herring as they migrate upstream or by deterring herring from navigating a "predator gauntlet". Our finding that larger herring were more prevalent in downstream areas ran counter to our predictions that size structure would be skewed towards larger herring in upstream areas due to their presumed higher energetic reserves and attendant ability to make more sustained upstream migrations. Given that larger fish are more likely to be experienced repeat spawners with a greater faculty for selecting appropriate spawning habitat, the concentration of larger fish in more

downstream areas further bolsters the hypothesis that these areas are important spawning habitats; it may also suggest that Striped Bass predation may be selectively concentrated on larger herring, thus removing them from the population before they can reach Holyoke. The relatively abundant aggregations of larger herring in downstream areas also suggests that these areas are making a significant contribution to production of the age-0 cohort, certainly dwarfing that made by the relatively few fish migrating above the Holyoke Dam. Overall, our findings suggest that a monitoring program based solely on sampling of the run at Holyoke Dam is unlikely to provide an accurate picture of herring abundance and demography in the lower Connecticut River.

We also found evidence of substantial within-year temporal structuring of the Connecticut River Blueback Herring run: early migrants to our study area were larger and more likely to be female fish. The greater prevalence of larger fish in early samples met our predictions and is consistent with other studies of river herring runs. For instance, Libby (1981) reported that mean length of Alewives migrating to the Damariscotta River fishway during 1977-79 were generally largest and oldest during the early portion of the migration season in early May. Cooper (1961) reported that mean length of Alewives migrating to Pausacaco Pond in Rhode Island steadily decreased over the course of the migration season, and that late migrants were on average 10% smaller than early migrants. However, our finding that early migrants were more heavily composed of female fish ran counter to our prediction and is not consistent with previous studies that have reported a higher prevalence of male fish during the early portion of the spawning season (Cooper 1961; Havey 1961; Kissil 1974; Libby 1981; Rideout 1974). The preponderance of larger females in the early portion of the spawning season may reflect condition-dependent breeding, in which larger individuals are energetically capable of migration to the spawning grounds at an earlier date, while smaller individuals must delay migration until sufficient energetic stores have been acquired (Schultz et al. 1991). The prevalence of larger female fish, which likely make an outsized contribution to annual reproductive output of the population, in the early portion of the migration season suggests that conservation measures (e.g. fishery closures) during this early period may make a disproportionate impact on future population growth; similarly, stressors (e.g. predation) or negative

environmental conditions (e.g. riverine flooding events that negatively impact egg or larval survival) during this early period may have significant negative consequences for future population states.

Our study clearly demonstrates the utility of demographic data for river herring conservation planning. We demonstrated that the Connecticut River blueback herring run is currently experiencing truncation of age and size structure as well as loss of iteroparity, a condition that may dampen population reproductive potential and resilience. However, we observed substantial inter-annual variation in demography, in contrast to our previous study of an Alewife run to a small coastal pond in close geographical proximity – suggesting that run sizes to a large river such as the Connecticut River may be driven to a greater extent by year class dynamics mediated by abiotic factors. Our observations of substantial temporal and spatial structuring of the Connecticut River run call into question the utility of biological monitoring at a fishway situated relatively far upstream, and also suggest that the habitat situated upstream of this fishway may currently be of minimal value to Blueback Herring in their state of depressed abundance. In particular, the spatial structuring of herring demography in our study area is consistent with the "striped bass hypothesis" (Savoy and Crecco 2004), suggesting that striped bass predation may be a significant source of mortality for this run and may alter habitat use.

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Figures

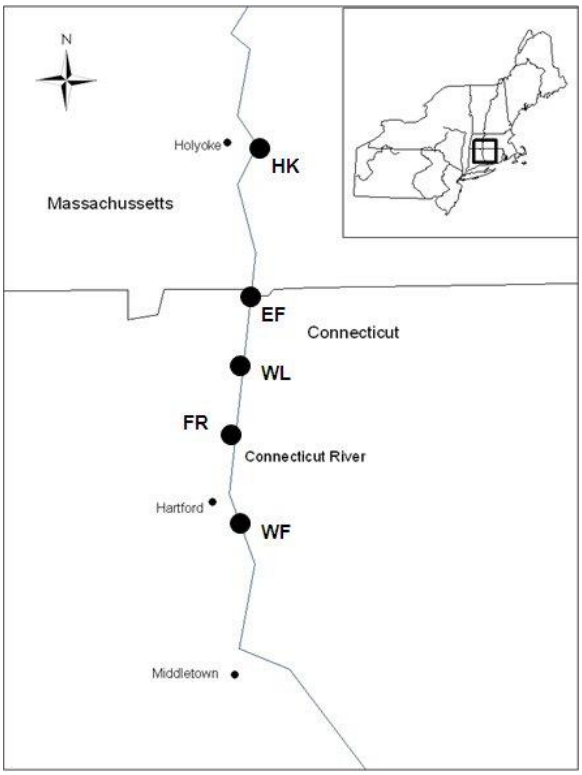

Figure 1 Map of the study area in the Connecticut River in northern Connecticut and southern Massachusetts. The five standard sites electrofished in 2005-07 are indicated: WF (Wethersfield), FR (lower Farmington River), WL (Windsor Locks), EF (Enfield), and HK (Holyoke).

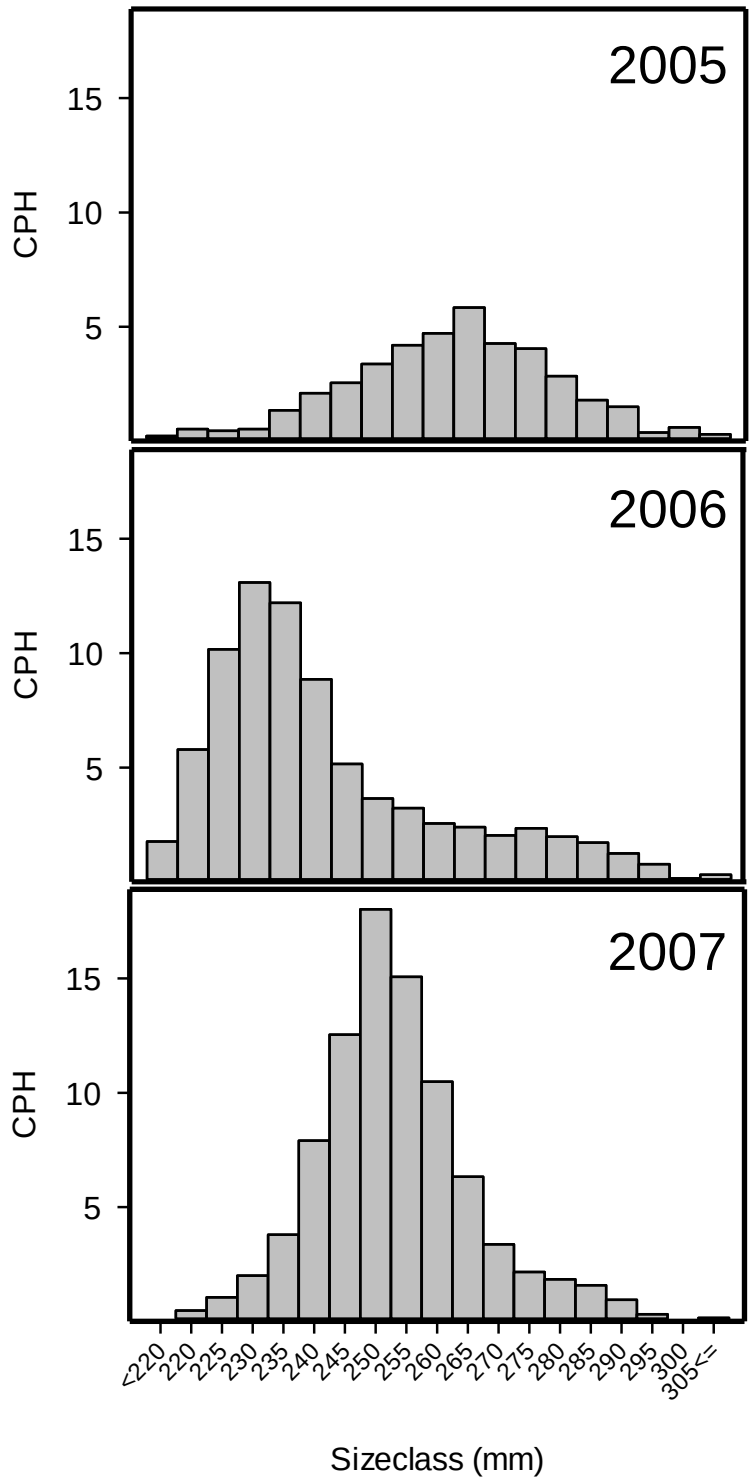

Figure 2 Size structure of Blueback Herring collected during 2005-07.

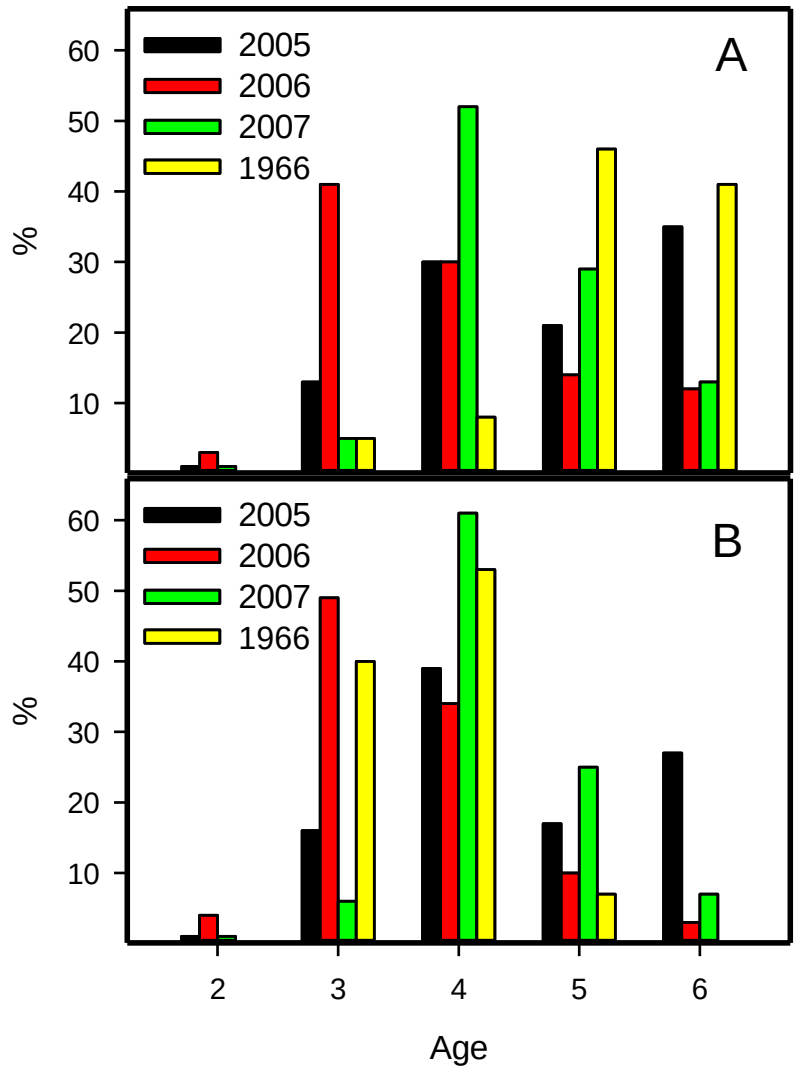

Figure 3 Age structure of all Blueback Herring (A) and virgin Blueback Herring (B) collected during 2005-07 (our study) and 1966-67 (Loesch 1969; Marcy 1969).

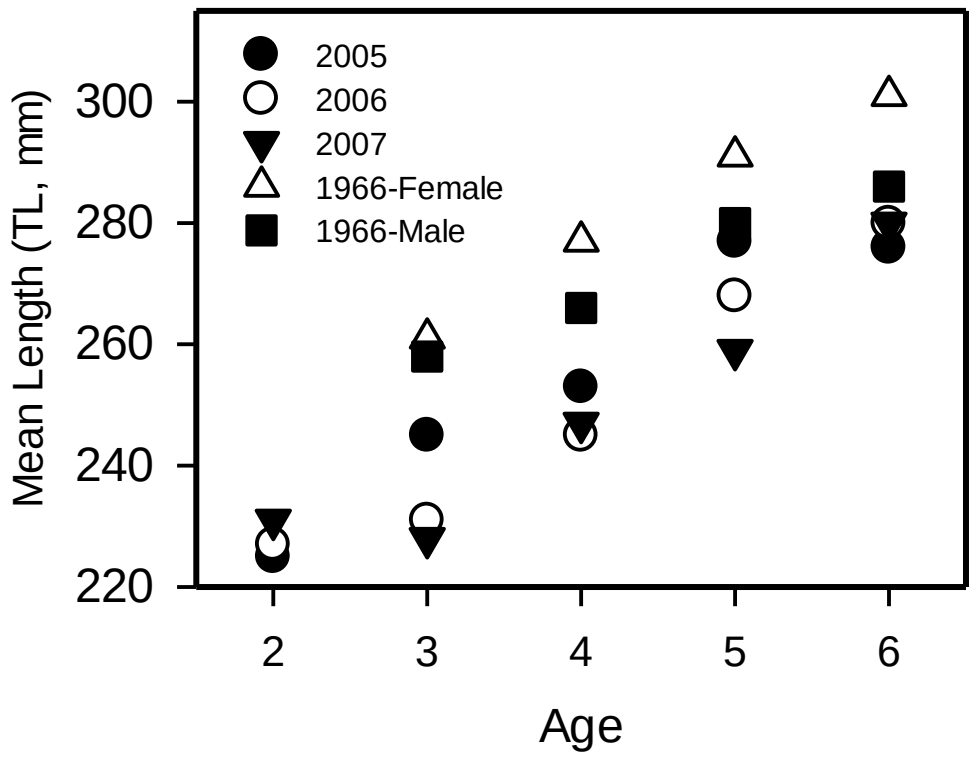

Figure 4 Mean length-at-age of Blueback Herring collected during 2005-07 (our study) and 1966-67 (Loesch 1969; Marcy 1969).

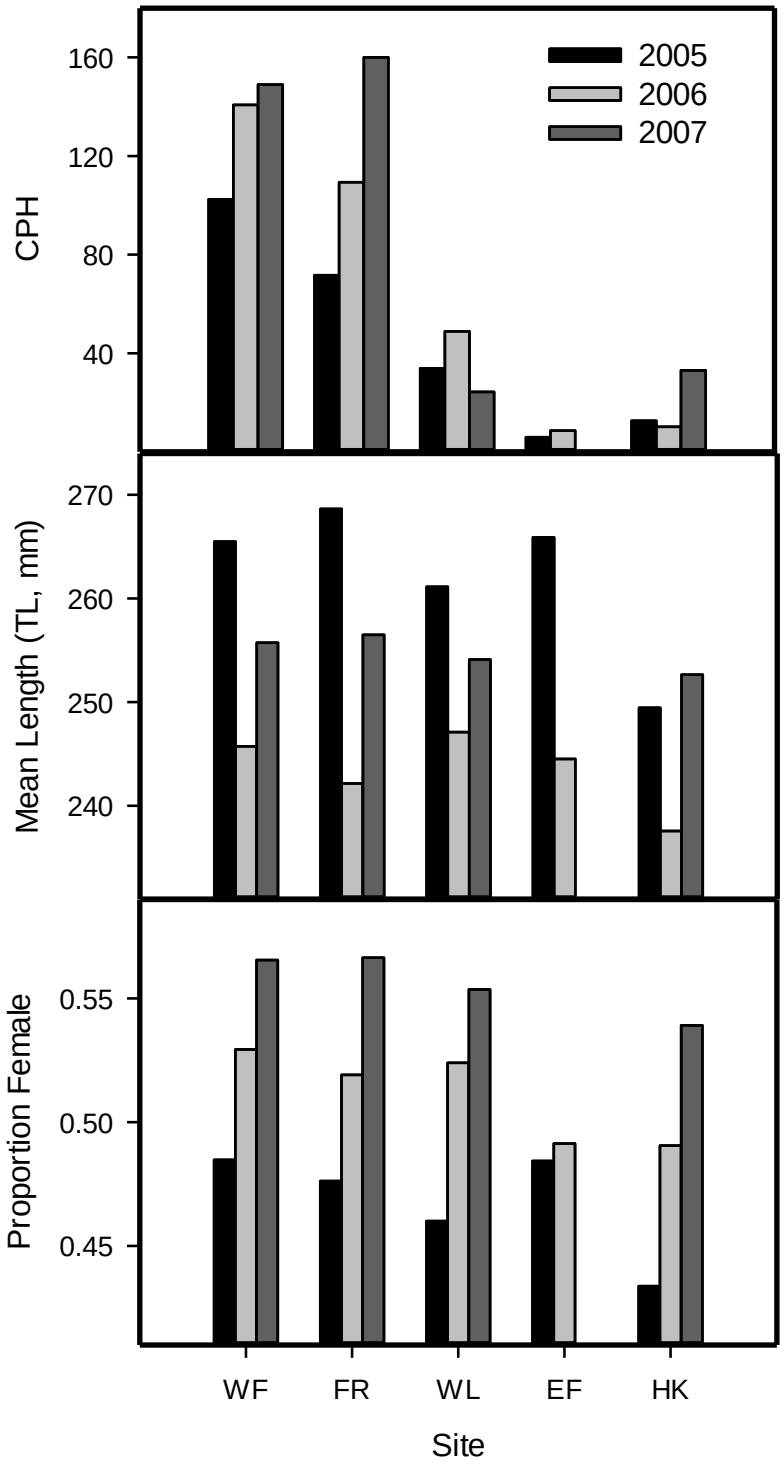

Figure 5 Mean electrofishing catch-per-hour (CPH), mean length (mm, TL), and proportion female Blueback Herring at the five study sites during 2005-07. Enfield (EF) is excluded in 2007 due to limited sampling.

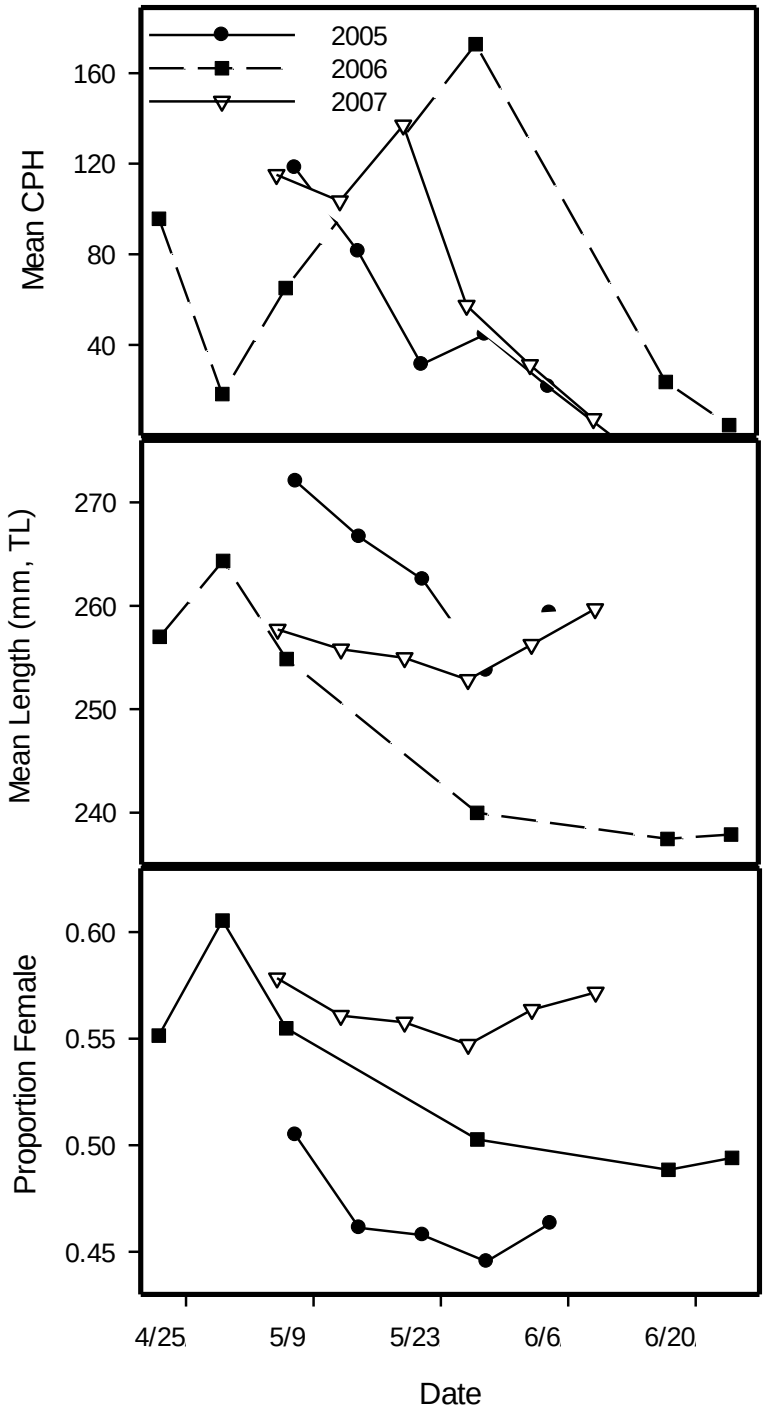

Figure 6 Mean electrofishing catch-per-hour (CPH), mean length (mm, TL), and proportion female Blueback Herring by calendar week during 2005-07. Points on the graphs correspond to the starting date (Sunday) of each calendar week during which sampling nights were conducted in each year.

Chapter 3

Striped Bass consumption of Blueback Herring during vernal riverine migrations: does relaxing harvest restrictions on a predator help conserve a prey species of concern?

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Abstract

Anadromous blueback herring (*Alosa aestivalis*) are declining throughout much of their range, and fishery closures in some systems have failed to produce population recovery. A potential contributing factor is increased predation pressure from sympatric striped bass (*Morone saxatilis*). We integrated data on the predator-prey interaction between striped bass and blueback herring during vernal migrations into the Connecticut River with data on the in-river striped bass fishery to assess the potential for mitigation of blueback herring mortality via increased striped bass harvest. Striped bass abundance, size structure, diets, and angler catches were assessed within a river segment during spring of 2005-08. We estimate that striped bass consumed 400,000 blueback herring (90% CI = 200,000-800,000) annually in our study area during the spring migration season. The predator-prey interaction between striped bass and blueback herring was predator-size-dependent; herring were most commonly found in stomachs of striped bass between 650-999 mm TL. Intermediate size classes (650-799 mm) made the greatest contribution to population-level consumption. Highly abundant small striped bass (400-549 mm) consumed herring infrequently yet still made substantial contributions to population-level consumption. Anglers caught 17,000 striped bass in our study area during March-June of 2008; only 11% of these fish could be harvested under the current 28" minimum length limit. Allowing anglers to harvest up to 15,000 sub-legal striped bass from a "bonus harvest" slot limit would reduce annual predatory losses of blueback herring by up to 10%. Alternately, a smaller bonus harvest of legal-sized striped bass could achieve reductions in consumption of up to 7%. The recreational fishery in our study area, however, may not be intense enough to realize such harvest levels.

Introduction

Fishery closures may fail to produce significant recovery of depleted fish populations (Dempson et al. 2004; Hutchings and Reynolds 2004). Factors potentially contributing to recovery failure include maladaptive changes in life history traits (Hutchings 2005; Walsh et al. 2006), release of interspecific competitors (Swain and Sinclair 2000; Link and Garrison 2002), and intensified predation (Bailey and Houde 1989; Walters and Korman 1999). Predation is of particular concern to fisheries managers as depensation (a decline in per-capita population growth rate) can occur when predators drive prey to low abundances (Shelton and Healey 1999; Frank and Brickman 2000). Populations subject to depensation often shift into domains of population behavior that are unresponsive to management, and can even decline towards extinction (Hilborn and Walters 1992; Spencer 1997; Walters and Kitchell 2001). In such situations, managers have additional options to improve prospects for population recovery if a directed fishery for key piscivores exists. Regulations that encourage increased predator harvests may reduce natural mortality of threatened prey species and help affect population recovery (Yodzis 2001). Studies evaluating the efficacy of such management strategies can aid in development of ecosystem-based approaches to fisheries management as the failure to adequately incorporate predation is an oft-cited shortcoming of traditional fisheries management models (Vetter 1988; Bax 1998; Moustahfid et al. 2009).

A predator-prey interaction of interest in this context is that between striped bass (*Morone saxatilis*) and anadromous river herring (alewife *Alosa pseudoharengus* and blueback herring *A. aestivalis*) in Atlantic coastal ecosystems. River herring make vernal spawning migrations or "runs" into many coastal rivers along the Atlantic seaboard (Loesch 1987). These seasonal aggregations provide an important source of forage for many marine, aquatic, and terrestrial predators (MacAvoy et al. 2000; Yako et al. 2000; Dalton et al. 2009; Walters et al. 2009). Recent range-wide declines in run size have prompted concerns over the loss of ecosystem services historically provided by river herring (Limburg and Waldman 2009). Concurrently, once-depressed coastal populations of predatory striped bass have increased to historic levels following the imposition of strict fisheries management measures during the 1980s (Atlantic States Marine Fisheries Commission 2009; see Fig. 1). Striped bass are prized by

recreational and commercial fishers alike and their recovery is a widely-celebrated example of successful fisheries management (Richards and Rago 1999). The ecological consequences, however, of increases in striped bass predation may be considerable. In particular, coastal populations of alosines, which are preferred prey of striped bass in many systems (Axon and Whitehurst 1985; Walter et al. 2003; Grout 2006), have likely experienced increased natural mortality resulting from striped bass predation (Hartman and Brandt 1995; Uphoff 2003; Heimbuch 2008). Striped bass management therefore has significant implications for river herring population dynamics. In particular, management scenarios producing increased striped bass harvests may ameliorate natural mortality operating on river herring populations and thus improve recovery prospects.

We selected the Connecticut River, a large river which empties into Long Island Sound in the Northeast United States of America, to study the predator-prey interaction between striped bass and river herring and assess the role that striped bass management can play in affecting river herring recovery. The pronounced decline of the blueback herring run in the Connecticut River segment between Hartford, Connecticut (the head of tide) and the Holyoke Dam in Massachusetts (the lowest mainstem dam) is well-documented; annual returns have declined four orders of magnitude at the Holyoke Dam over the last 25 years (United States Fish and Wildlife Service 2011; see Fig. 1). This and other regional declines prompted a river herring fishery closure in Connecticut in 2002, closely followed by closures in the neighboring states of Massachusetts and Rhode Island in 2005 (Davis and Schultz 2009). Despite the fishery closure, the Connecticut River blueback herring run shows no signs of recovery (Fig. 1). Striped bass, conversely, have become abundant in the Connecticut River during spring in recent decades (Fig. 1). Strong correlative evidence supports the hypothesis that increased predation by striped bass has recently contributed significantly to blueback herring declines in the Connecticut River (Savoy and Crecco 2004). Moreover, persistent striped bass predation may be preventing blueback herring recovery and could potentially have depensatory effects. Given current low prey abundances and the perceived importance of predation, the Connecticut River is a system in which reductions in predator abundance could reasonably be expected to produce a positive effect on a depressed prey population. Additionally, an intensive

springtime recreational fishery for striped bass exists along the entire river south of the Holyoke Dam (Jacobs and O'Donnell 2002; Davis et al. 2011). This fishery offers managers a mechanism to achieve reductions in predator abundance.

Recognizing the potential to reduce predatory pressure on a species of conservation concern and provide anglers a new harvest opportunity, the Connecticut Department of Energy and Environmental Protection (CDEEP) instituted experimental regulations on the spring recreational fishery for striped bass in the Connecticut River. The Connecticut fishery had previously been managed under blanket coast-wide striped bass regulations (28" minimum length limit, 2 fish daily creel limit). The experimental regulations instituted by CDEEP allowed anglers to harvest two striped bass per day within a 22-28" slot limit from the Connecticut portion of the Connecticut River during May and June. This "bonus harvest" program was created by transferring an unused commercial quota (approximately 24,000 lbs) to the recreational fishery; the bonus harvest was capped at 4,000 fish so as not to exceed the quota. A voucher system was instituted to maintain the bonus harvest within this annual limit. The bonus harvest was first implemented in 2011, after diet sampling and abundance estimates of striped bass described below revealed the potential for considerable predatory losses of blueback herring.

The goal of this study was to assess reductions in predatory losses of blueback herring that might be achieved through alternative management of the striped bass fishery in the Connecticut River. To quantify potential reductions, we integrated data on the trophic interaction with data on the recreational striped bass fishery in the Connecticut River. The specific objectives of this study were to: 1) assess striped bass abundance and size structure in the Connecticut River during the vernal migration; 2) quantify the prevalence of blueback herring in diets of striped bass among various predator sizes; 3) estimate population-level consumption of blueback herring by striped bass; 4) survey recreational anglers to estimate numbers and sizes of striped bass caught and harvested; 5) forecast reductions in population-level consumption under several hypothetical alternative management regulations.

Methods

Sampling for striped bass size structure, food habits, and absolute abundance

We collected striped bass by night-time boat electrofishing (Smith Root Model SR-18 equipped with a 5.0 GPP electrofisher and two SAA-6 electrode arrays) in the Connecticut River segment between Wethersfield, CT (near the head of tide) and the dam at Holyoke (a 64 km stretch hereafter referred to as the "study area", see Fig. 2), during spring 2005-08. We selected this river stretch for several reasons, including: 1) large, migratory striped bass are known to aggregate there during spring (Savoy and Crecco 2004; see Fig. 1); 2) striped bass predation on anadromous alosines has previously been documented in the area immediately below the Holyoke Dam (Warner and Kynard 1986); 3) it is small enough to permit weekly comprehensive sampling; and 4) its physical configuration (relatively narrow and shallow) facilitated boat electrofishing. Sampling began as soon as river stage permitted access, typically in early May, and ceased once striped bass catch rates became consistently low and/or river stage became too low for safe navigation in June. During 2005-07, we sampled the same five sites (Fig. 2) weekly, river conditions and equipment permitting. In 2008 sampling concentrated on the Windsor Locks site (see below).

Boat electrofishing is an effective gear for collecting warmwater fishes from the littoral zone of large rivers (Guy et al. 2009). Accordingly, we sampled fixed transects located parallel to the shoreline in near-shore, shallow habitat ($\leq$ 2 m depth). We classified available macro-habitats within the littoral zone at each site into six categories (mainstem, coves, tributaries, tailraces, cove/mainstem interface, tributary/mainstem interface, and tailrace/mainstem interface) and distributed electrofishing transects as evenly as possible across available macro-habitat types at each site. Transects were sampled by positioning the boat perpendicular to shore and drifting downstream with ambient current, although slow currents (<0.5 m/s) in some areas necessitated upstream shocking (Guy et al. 2009).

In 2005-2007 we assessed along-river relative abundance (as electrofishing catch-per-hour, or CPH), size structure, and food habits of striped bass. All striped bass collected were counted, measured (total length, or TL, in mm), and subjected to gastric lavage. We released all striped bass at the capture

location after on-board workup. Diet samples were placed on ice immediately after collection and frozen within 12 hours. After thawing, diet items were sorted to the lowest possible taxon. Stomachs yielding only fragmentary remains (scales or small number of bones) were not scored as containing prey because we assumed that these remains derived from prey consumed >24 hrs before sampling.

In 2008 we estimated striped bass absolute abundance via mark-recapture. Fish were captured and tagged by night-time boat electrofishing, and subsequently recaptured by night-time boat electrofishing and by anglers. We focused our tagging efforts exclusively on the Windsor Locks site (Fig. 2) to maximize the number of fish tagged (electrofishing CPH was consistently highest at this location in 2005-07, see Davis et al. 2009). We limited the mark-recapture effort to the month of May because the recommended study period length for closed population models is <1 month (see review by Pine et al. 2003). We tagged all striped bass ≥300 mm TL with a t-bar internal anchor tag. Tags featured a phone number for capture reports. We used two different tag colors to designate standard and high reward tags (worth $15 and $50, respectively) to estimate standard tag reporting rates (Pollock et al. 2001). Cooperating anglers phoned in capture date, location, and disposition (harvested or released) of recaptured striped bass. Absolute abundance of striped bass ≥300 mm TL ($\hat{N}$) was estimated using the Schnabel method (Hayes et al. 2007):

$$\hat{N} = \frac{\sum_{d=2}^{t} c_d M_d}{1 + R_e + R_{a,h} + R_{a,s}\lambda^{-1}} \qquad (1)$$

where: t = number of sampling days; c_d = total fish captured on sampling day d (by both anglers and electrofishing); M_d = number of tagged fish at large for sample day d; R_e = total recaptures obtained by electrofishing; $R_{a,h}$ = total angler returns of high reward tags; $R_{a,s}$ = total angler returns of standard reward tags and λ = the standard reward tag reporting rate, estimated as (Pollock et al. 2001):

$$\lambda = \frac{R_{a,s} T_h}{R_{a,h} T_s} \qquad (2)$$

where: T_h = total high reward tags released and T_s = total standard reward tags released. Every day in May was treated as a sampling day. The total catch (c_d) of striped bass ≥300 mm on each day was estimated as the sum of electrofishing catch (if electrofishing was conducted) and estimated angler catch. Electrofishing catch was known; catch by recreational anglers was estimated from creel survey data (see *Assessing the recreational fishery*). For sample days without creel surveys, catch was estimated as the mean catch for that day-type stratum (weekend vs. weekday) during May. Because we conducted tagging and creel surveys only in the Connecticut portion of the study area, we similarly restricted angler recaptures used in estimating abundance ($\hat{N}$) to those obtained between Wethersfield, CT and the Massachusetts border (42 km); to expand the abundance estimate to the entire study area, we standardized $\hat{N}$ to river kilometer and then multiplied by the length of the study area (64 km).

Estimating population-level consumption of blueback herring

We modeled striped bass population-level consumption as a function of our tag-based 2008 population estimate, and size structure and diet estimated from 2005-2007 electrofishing samples. The population of striped bass ≥300 mm TL was divided into 50 mm size classes, lumping all fish ≥1000 mm. The number of striped bass in each 50 mm size class ($\hat{n}_i$) was estimated as:

$$\hat{n}_i = \hat{N}\left(\sum_j p_{i,j} w_j\right) \quad (3)$$

where: $\hat{N}$ = estimated absolute abundance of striped bass from equation 1, expanded to the entire study area; $p_{i,j}$ = proportion of striped bass in size class *i* at site *j* (across all 2006-07 electrofishing samples at site *j*; 2005 samples were excluded because mechanical issues with the electrofishing boat in that year reduced capture efficiency for larger fish and thus biased estimates of size structure); and w_j = weighting factor for site *j* calculated as:

$$w_j = \frac{\overline{E}_j}{\sum_j \overline{E}_j} \quad (4)$$

where: $\overline{E}_j$ = mean electrofishing CPH of striped bass ≥300 mm TL at site *j* (across all 2006-07 electrofishing samples at site *j*). Weighting factors were used to correct for potential biases introduced by unequal numbers of sampling nights across sites during 2006-07. The population-level consumption ($\widehat{C}$) of blueback herring by striped bass ≥300 mm TL over the vernal migration period was then estimated as:

$$\widehat{C} = V\sum_i \left(\widehat{n}_i \sum_j q_{i,j,1} w_{i,j} \right) + \left(2\left(\widehat{n}_i \sum_j q_{i,j,2} w_{i,j} \right) \right) \quad (5)$$

where: V = number of days in the migration season; $q_{i,j,1}$, $q_{i,j,2}$ = proportion of diet samples from striped bass in size class *i* at site *j* that contained 1 or 2 blueback herring, respectively (across all diet samples collected in 2005-07); and $w_{i,j}$ = weighting factor for size class *i* at site *j*. We restricted diet outcomes to 1 or 2 herring (i.e. we assumed that striped bass consumed a maximum of 2 herring per day) as <5% of striped bass stomachs with herring contained more than two.

We quantified uncertainty in our population-level consumption estimates via a Monte Carlo randomization (Hilborn and Mangel 1997). For each of 10,000 model runs, simulated data on absolute abundance, size structure, and diet composition were created using appropriate probability distributions. Striped bass abundance ($\widehat{N}$ in equation 1) was randomized by sampling the total number of recaptures (sum of R_e, $R_{a,s}$, and $R_{a,h}$; see equation 1) from a Poisson distribution with mean λ = total number of recaptures (we used a Poisson distribution because we obtained <25 recaptures, see Hayes et al. 2007). Size structure was randomized by sampling the number of striped bass measured during 2006-07 electrofishing samples from a multinomial distribution parameterized with observed proportions-at-length ($\sum p_{i,j} w_j$ from equation 3). The randomly sampled abundance and size distribution dataset yielded a randomized vector of proportions-at-length that was substituted for observed proportions-at-length in equation 3. Diet composition for each striped bass size class was randomized by sampling the number of striped bass in the size class that was lavaged in 2005-07 from a multinomial distribution parameterized with observed proportions of striped bass in size class *i* that consumed 0, 1, and 2 herring ($\sum q_{i,j,n} w_{i,j}$ from equation 5). The randomized matrix of proportions of striped bass consuming 0, 1, and 2 herring was

substituted for observed diet proportions in equation 5. The number of days in the vernal migration season (*V* in equation 5) was randomized by sampling integers between 30 and 50 from a uniform distribution (based on observed season lengths during 2005-08, see Davis et al. 2009). Randomized datasets were created in SAS (SAS v. 9.3) using the IML Procedure (multinomial) and the Rand function (Poisson). We summarized results of the Monte Carlo simulation as median consumption rates with 5% and 95% confidence limits (i.e. with a 90% confidence interval [CI]).

Assessing the recreational fishery

A "bus stop" design creel survey (Jones and Robson 1991; Pollock et al. 1994) conducted by the CDEEP in 2008 estimated recreational catches of striped bass in the Connecticut River between Middletown, Connecticut, and the Massachusetts border (Davis et al. 2011). The creel survey segment was divided into two independent survey zones (Zone 3: Middletown, CT to Hartford, CT; Zone 4: Hartford, CT to the Massachusetts border). The survey within each zone was stratified by two month seasons (Season 1: March-April; Season 2: May-June; Season 3: July-August; Season 4: September-October) and secondarily by day type (weekend vs. weekday) within each season. Creel agents surveyed each zone on two weekdays, randomly selected, and both weekend days during each calendar week. Surveys started either in the morning (6:00 or 7:00) or afternoon (13:00 or 14:00) and lasted for six hours; an equal number of morning and afternoon surveys were conducted within each day-type stratum during each month. No night-time surveys were conducted.

During each bus stop survey, clerks counted all shore anglers and boat trailers (as a proxy for boat anglers) at a series of access points. Other regularly-conducted supplementary surveys estimated the proportion of trailers that were attributable to anglers and the proportion of shore angler effort occurring at sites within a zone that were not surveyed by the bus stop survey (Davis et al. 2011). Clerks also interviewed individual anglers for data on trip lengths and numbers/sizes of all fish caught. All harvested fish in an interviewee's possession were measured by the clerk (TL, cm). Interviewees were then asked to estimate TL of any released fish in inches.

The time interval count estimator and the ratio-of-means estimator (Pollock et al. 1994; Davis et al. 2011) were used to estimate total angler effort (angler-hrs) and mean angler catch rate (CPH) of various fish species, respectively, for each bus stop survey day. Both quantities were estimated separately for each angling mode (boat vs. shore); total catch for each mode on each bus stop survey day was then estimated as the product of angler effort and mean CPH. Total harvest for each mode was estimated in an analogous manner using estimates of harvest-per-hour instead of CPH. Total catch or harvest ($\hat{Y}$) of each species for each mode for an entire 2-month season was estimated as (Pollock et al. 1994; Davis et al. 2011):

$$\hat{Y} = D\sum_{w}\left(\frac{n_w}{D}\right)\bar{y}_w \quad (6)$$

where: D = number of days in the season; n_w = number of days in day-type stratum w and $\bar{y}_w$ = sample mean of catch or harvest for day-type stratum w. The variance of the total catch or harvest estimate [$Var(\hat{Y})$] for the season was estimated as (Pollock et al. 1994; Davis et al. 2011):

$$Var(\hat{Y}) = D^2\sum_{w}\left(\frac{n_w}{D}\right)^2 \frac{S^2{}_w}{d_w}\left(\frac{n_w - d_w}{d_w}\right) \quad (7)$$

where: $S^2{}_w$ = sample variance of catch or harvest for day-type stratum w and d_w = number of days sampled in day-type stratum w. The standard error of the total catch or harvest estimate was estimated as the square root of the variance (Pollock et al. 1994; Davis et al. 2011).

We approximated total angler catch and harvest of striped bass in the Connecticut portion of our study area during the 2008 spring migration season by summing Season 1-2 (March-June) catch and harvest estimates for both fishing modes from Zones 3-4. Standard errors of overall catch and harvest estimates were estimated as the square root of the sum of $Var(\hat{Y})$ across zones/seasons/modes. Zone 3 only partially overlapped our study area (Fig. 2); we therefore estimated the percentage of angler effort occurring north of Wethersfield, CT in Zone 3 during Seasons 1-2 (64%) and adjusted totals and variances of striped bass catch and harvest in Zone 3 accordingly.

Forecasting reductions in consumption under alternative management regimes

We modeled potential reductions in blueback herring consumption under alternative management regimes for the striped bass fishery in the Connecticut portion of our study area. Each management scenario was modeled as a "bonus" harvest program – i.e. allowance of harvest additional to baseline harvest already occurring under the existing 28" minimum length limit/2 fish daily bag limit. Scenarios were modeled on the bonus harvest program instituted by CDEEP. Five bonus harvest slot limit scenarios targeting sub-legal size classes were modeled: 22-27" (560-690 mm), 20-27" (510-690 mm), 16-27" (406-690 mm), 16-23" (406-584 mm), and 16-21" (406-533 mm). Annual harvest under each slot limit was varied from 5,000 to 20,000 fish in increments of 5,000 (i.e. 10,000 model runs at each harvest level).

To model reductions in blueback herring consumption under each bonus harvest scenario (combination of slot limit and annual harvest level), the randomized blueback herring consumption model was run 10,000 times with an additional input that described striped bass removals. For each model run, the number of striped bass harvested from each 50 mm size class vulnerable to the slot limit was randomly sampled from a multinomial distribution parameterized with estimated proportions of the annual harvest that would be taken from each vulnerable size class. Proportions of annual harvest taken from each vulnerable size class ($\hat{r}_i$) were estimated as:

$$\hat{r}_i = \frac{\hat{Y}_i}{\sum_i \hat{Y}_i} \qquad (8)$$

where: $\hat{Y}_i$ = estimated angler catch of striped bass from size class *i* in the Connecticut portion of the study area during March-June 2008. Estimated harvests within each vulnerable size class were subtracted from the abundance of striped bass in the class ($\hat{n}_i$ from equation 3) prior to each model run.

We also modeled alternative management scenarios with an unchanged 28" minimum length limit but increased harvest, such as might be achieved by increasing the existing bag limit. Model runs were conducted in which the total harvest of striped bass ≥710 mm TL (28") from the Connecticut portion of the study area during March-June 2008 was increased by a factor of 2-4. These model runs were

conducted in an analogous manner to those for the bonus harvest slot scenarios; the number of striped bass harvested from each vulnerable size class was modeled as a multinomial variable, and the estimated harvest was subtracted prior to each model run.

We were interested in the feasibility of various levels of annual harvest under each of the modeled regulation scenarios. Specifically, we wished to address the question: given the available data on angler catch and harvest of striped bass during spring 2008, how likely is it that anglers in the Connecticut portion of the study area could catch and harvest enough striped bass to meet the annual harvest goal under various alternative regulation scenarios? To address this question, we calculated an index of "Harvest Increase" (*HI*) that compared the size of annual harvests from vulnerable size classes for each modeled bonus harvest scenario to angler catches from those size classes in spring 2008:

$$HI = \frac{1}{m}\sum_{x}\left(\frac{1}{k}\sum_{i}\frac{H_{i,x}}{\widehat{Y}_i}\right) \qquad (9)$$

where: m = number of model runs (10,000); k = number of size classes vulnerable under the regulation scenario and $H_{i,x}$ = number of striped bass harvested from vulnerable size class i in model run x. If $HI = 1$ for a bonus harvest scenario, then on average Connecticut anglers would have to harvest as many vulnerable striped bass as they caught during spring 2008 to meet the annual harvest goal; higher *HI* scores indicate lower feasibility of achieving annual harvest goals.

Results

Striped bass size structure, food habits, and absolute abundance

The population of striped bass in our study area during 2006-07 was composed primarily of sub-legal fish (Fig. 3a). Approximately three quarters of the 606 striped bass ≥300 mm (12") we collected were smaller than 710 mm TL (28"). The modal sizes were 350–499 mm (13 – 19"); a long tail of declining proportions-at-length culminated in a slightly higher proportion in the aggregated class of fish ≥1000 mm (39").

Consumption of blueback herring was predator size dependent (Fig. 4). Blueback herring were eaten by striped bass over most of the size range we captured by electrofishing. Herring were most

commonly eaten by 650-999 mm TL (25–39") striped bass; herring were recovered from 19% of these fish, and most of the striped bass containing more than one herring were in this size range (Fig. 4).

We tagged a total of 500 striped bass in Windsor Locks during May 2008. A total of 16 recaptures were recorded in the Connecticut portion of our study area during May (13 by anglers, 3 by electrofishing; an additional 5 tags were returned by anglers during May from areas outside the Connecticut portion of the study area). We increased the total return of standard ($15 reward) tags from six to nine to reflect an estimated 68% angler reporting rate, bringing the May recapture total to 19. The total daily catch of striped bass during May 2008 ranged from 48 to 705 fish (mean = 196, median = 138). The Schnabel model (equation 1) yielded an estimate of 81,598 striped bass ≥300 mm (95% CI = 53,332-130,557) in the Connecticut portion of the study area, or approximately 1,951 fish/river km. Expanding this estimate by the length of the entire study area, we estimate that 125,536 striped bass ≥300 mm (95% CI = 82,050-200,857) were present during May 2008.

Population-level consumption of blueback herring

We estimate (equation 5) that striped bass consumed 370,582 blueback herring. The Monte Carlo model simulation of herring consumption estimated a median striped bass population-level consumption of 395,062 blueback herring (90% CI = 178,153-791,181; Fig. 5). Striped bass in the 450 mm (17-19"), 650 mm (25-27"), and 750 mm (29-31") size classes consumed the greatest number of herring, accounting for a mean of approximately 40% of population-level consumption across 10,000 model runs (Fig. 6). Striped bass between 850-999 mm TL (33-39"), despite high per-capita rates of blueback herring consumption (Fig. 4), made a small contribution to population-level consumption (Fig. 6). Conversely, smaller striped bass that ate herring infrequently (Fig. 4) nonetheless made large contributions to population-level consumption (Fig. 6) as a result of their high abundances (Fig. 3).

Recreational fishery

Striped bass angling dominated the recreational fishery in the river stretch between Middletown, CT and the CT/MA border during March-June 2008: 64% of anglers targeted striped bass. We estimate that anglers caught 17,077 striped bass (SE = 3,701) in the Connecticut portion of our study area during

March-June 2008, of which 14,122 were ≥300 mm TL. The recreational catch was composed overwhelmingly of fish <710 mm (28"; Fig. 3b). We estimate that only 11% of striped bass landed were legal-sized (≥710 mm or 28"), and 77% of striped bass landed were <500 mm (20"). We estimate that anglers harvested 70% (1,311 striped bass) of legal-sized striped bass caught, but this harvest estimate was imprecise (SE = 764).

Reductions in consumption under alternative management regimes

Bonus harvest scenarios that yielded the greatest reduction in herring consumption were the least likely to be fulfilled. Bonus slot limits operating on larger fish yielded the greatest reduction in median total consumption of blueback herring (Fig. 7). At an annual harvest level of 15,000 striped bass, the 22-27" and 20-27" bonus slots yielded 11% reductions in median consumption; slots operating on smaller fish yielded about 8% reductions (Fig. 7). Such sizeable annual harvest of larger fish, however, may be difficult to achieve. For instance, we estimate that an annual harvest of 15,000 striped bass from a 22-27" bonus slot operating in the Connecticut portion of the study area would require anglers to achieve a harvest 12-13 times larger than the estimated catch of slot-sized striped bass in the Connecticut portion of the study area during March-June 2008 (Fig. 8). Broader slot limits permitting harvest of smaller striped bass would have a greater probability of achieving total harvest goals (Fig. 8). The broadest slot limit (16-27") provided the greatest reduction in median consumption amongst slots that operated on smaller fish (Fig. 7), and had the best (lowest) *HI* scores (Fig. 8). Harvest of an additional 1,000-4,000 legal-sized (≥28") fish provided reductions in blueback herring consumption comparable to those achieved by bonus slot limits at much higher levels of annual harvest (Fig. 7), and appeared relatively feasible (Fig. 8).

Discussion

Striped bass size structure, food habits, and absolute abundance

Our study documented a large contingent of striped bass (estimated at >100,000 fish at a mean density approaching 2,000 fish/river km) above the head of tide in the Connecticut River. The appearance of striped bass in this area is coincident with the vernal spawning migration of blueback herring. Electrofishing catch rates of striped bass generally declined to low levels in our study area by mid-June

(Davis et al. 2009), and recreational catches of striped bass were negligible in March and July-October (Davis et al. 2011). In addition, anglers returned tags from a wide range of coastal locations during summer and fall (Davis et al. 2009). Taken together, these observations strongly suggest that most of the striped bass migrating to our study area are members of the coastal population that emigrate at the conclusion of spring. We also showed that these migratory predators prey on blueback herring while in the study area. Given that striped bass opportunistically target spawning aggregations of anadromous alosines in other systems (Trent and Hassler 1966; Manooch 1973), striped bass likely migrate to the Connecticut River at least in part to exploit spawning aggregations of blueback herring. Recent observations of increasing numbers of apparently non-spawning striped bass migrating into multiple coastal rivers in the Northeastern United States during spring (Grout 2006) support the hypothesis that such vernal feeding forays are a widespread consequence of the recent coastal striped bass recovery. Unfortunately, there are no long-term data on the vernal abundance of striped bass in the Connecticut River to provide our discussion of the current situation with a historical perspective.

Interactions between the Connecticut River blueback herring population and striped bass are not limited to consumption of adult herring during the vernal migration. Sub-adult (i.e. ≤age 7) striped bass are present in the Connecticut River estuary (south of our study area) for much of the year (Jacobs et al. 2004; Savoy and Crecco 2004) and presumably prey upon young-of-year alosines while there (Hartman and Brandt 1995; Hartman 2003). However, we regard the vernal episode of adult herring consumption as that having the highest potential impact on herring populations. Observed shifts in recent decades among river herring towards fewer old spawners, fewer repeat spawners and earlier age at maturation suggests that mortality has increased among older age classes (Davis and Schultz 2009). Moreover, studies of striped bass diets during coastal residence in nearby Massachusetts found low incidence of alosine prey (Nelson et al. 2003).

There were several potential sources of bias in our estimates of striped bass abundance, size structure and food habits. We limited our sampling to the littoral zone where the boat electrofisher would be effective (Guy et al. 2009). We therefore did not sample all available habitats at each site, and also

sampled a different proportion of the available habitat at each site. We could not estimate size-selectivity of the boat electrofisher, because alternate gears did not yield sufficient catch for comparison. The Schnabel mark-recapture model used to estimate striped bass abundance assumes population "closure" during the study period (Lukacs 2009). We assumed population closure at the height of the migration in May. However, tag returns from outside the study area as well as variation in electrofishing catch rates (CPH within the study area generally varied by a factor of 1-4 during May 2006-07; see Davis et al. 2009) indicate that some movement to and from the study area occurred during this period; our abundance estimates are therefore biased to an unknown degree. Additionally, the underlying assumption of complete mixing of tagged fish into the target population (Seber 1982) may have been violated because we released all tagged fish at the Windsor Locks site. Sampling requirements of more robust models (e.g. Jolly-Seber) could not logistically be accomplished with our available resources within the relatively short temporal window of the vernal migration (Kendall 2009; Schwarz and Arnason 2009). Finally, our approach to expanding the estimate of striped bass abundance in the Connecticut stretch to the entire study area assumed that mean density of striped bass in Connecticut adequately approximated density in Massachusetts. This assumption was necessary because we did not sample the majority of the Massachusetts stretch (Fig. 2). If striped bass density in Massachusetts was significantly higher or lower than in Connecticut, our expanded abundance estimates would be biased low or high, respectively.

Population-level consumption of blueback herring

We estimate that the contingent of striped bass migrating above the head of tide in the Connecticut River currently consumes approximately 400,000 blueback herring each spring. This predatory loss is sizeable; our estimates of population-level consumption are comparable to the number of blueback herring passing Holyoke Dam during peak years in the late 1980s (Fig. 1). Our estimate of consumption may be somewhat conservative because we assumed that striped bass consumed a maximum of two herring daily. We made this assumption because <5% of striped bass stomachs sampled with herring prey contained more than two; the additional herring prey within those stomachs were generally at an advanced stage of digestion, suggesting they had been consumed >24 hrs before sampling.

Nonetheless, larger striped bass are certainly capable of consuming more than two herring per day if presented the opportunity. Multiple anglers interviewed for the creel survey related anecdotes of finding >2 herring in stomachs of harvested striped bass. Our consumption estimates did not explicitly account for the effects on gastric evacuation rates of water temperature, predator size, or meal size (Elliot and Persson 1978; Elliot 1991; Temming and Andersen 1994). This simplification was necessary because no information is available on the temperature-dependence of gastric evacuation rates for large striped bass consuming large piscine prey items.

Recreational fishery and reductions in consumption under alternative management

Manipulation of striped bass harvest regulations in the Connecticut River can reduce predation on blueback herring. Reductions in predation mortality of 4-10% can be achieved in our study area if Connecticut anglers harvest 10,000-15,000 currently sub-legal striped bass. Similar levels of mortality reduction could be realized with an additional harvest of several thousand currently legal-sized (>28") striped bass. The recent survey of the fishery, however, suggests that these levels of additional annual harvest may be improbable. Under most modeled scenarios, Connecticut anglers would have to harvest as many or more (in some cases, >10 times more) striped bass from vulnerable size classes as they caught during spring 2008 to meet bonus harvest targets. Nonetheless, many anglers harvest striped bass when presented with the opportunity; anglers harvested 70% of legal-sized fish caught during spring 2008. Many anglers interviewed during the creel survey communicated a desire to harvest presently sub-legal fish because smaller fish are more palatable and contain lower levels of contaminants. A bonus harvest program could therefore increase angling effort by current Connecticut River anglers, and may even attract new anglers. Such a change in angler behavior could make annual bonus harvests of the magnitude described here more realistic.

Our model assumed that all harvested striped bass would be removed by anglers before consuming any herring prey and that there would be no compensatory natural mortality of blueback herring (i.e. we assumed that all herring "saved" under a bonus harvest scenario would survive for the duration of the migration season). These simplifying assumptions were necessary as the data required to

quantify these factors were too coarse (in the case of temporal trends in angler catch) or unavailable (daily probabilities of herring survival).

Management Implications and Future Directions

Identifying and mitigating natural mortality of river herring is a primary concern for regional fisheries managers because populations have not recovered following fishery closures. If vernal striped bass predation is the primary factor regulating blueback herring population size and compensatory predation by other predators is minimal, then the relatively small reductions in annual mortality described here may accrue significant long-term benefits to the Connecticut River blueback herring population. Blueback herring are a short-lived, highly fecund species (Loesch 1987), and thus their populations have high resilience and intrinsic growth rates (Gotelli 2001). Even relatively small reductions in annual mortality can therefore produce appreciable population growth on a decadal scale. Increased in-river harvests of striped bass may cause a sustained decrease in the size of the striped bass vernal migration into the Connecticut River. The likelihood of this hypothesis rests in part on whether the group of striped bass migrating to the Connecticut River is a true "contingent" – i.e. a distinct, persistent sub-group of the coastal stock defined by a divergent seasonal migration pattern (Clark 1968; Secor 1999). Striped bass have shown fidelity to non-natal foraging sites (Mather et al. 2009) and natal site (Mansueti 1961; Nichols and Miller 1967). Although it has not been directly demonstrated, spawning of striped bass in the Connecticut River is possible: we captured ripe-running fish of both sexes during our study, and small, presumably young-of-year fish have been collected in the river during fall (Jacobs et al. 2004). Future studies assessing whether the Connecticut River is a spawning site and the degree of inter-annual site fidelity will elucidate whether the vernal striped bass migration truly represents a contingent susceptible to reductions through increased harvest.

Other considerations suggest that an immediate recovery of blueback herring in the Connecticut River is unlikely. Most alternative management scenarios produced reductions in consumption of <10%, and those producing greater reductions appear to be relatively improbable given the current condition of the fishery. Even if herring consumption decreases because of higher striped bass harvest, the herring

population may not rapidly recover. The steep declines in blueback herring run size noted during the late 1980's/early 1990's occurred when vernal striped bass abundances were probably well below the reduced abundances modeled here, judging from data on coastal abundance (Fig. 1). The management strategies outlined here will also not address other potential stressors to the herring population such as bycatch in marine fisheries (Cieri et al. 2008), and also do not take into account the possibility that increased consumption by other predators will compensate for reductions in striped bass consumption.

Our findings illustrate the important roles that predator size and selectivity operating at multiple trophic levels (given that anglers are essentially top-level predators in this system) play in determining the trophic implications of fisheries management scenarios. Increased abundance of desirable size classes is a common management goal that is typically achieved by modulating the magnitude and size-selectivity of fishing mortality (Noble and Jones 1999). Resulting changes in the size distribution of managed fish populations have implications for populations at lower trophic levels because predator size plays an important role in determining prey selection and per-capita consumption rates (Juanes et al. 1993; Scharf et al. 1997; Scharf et al. 1998; Hartman 2000; Johansen et al. 2004; Rudershausen et al. 2005). Management outcomes may not be readily inferred from examination of one or more of these factors at a single trophic level. For instance, our diet data revealed that smaller striped bass (400-549 mm) consumed blueback herring infrequently; however, when population abundance and size structure were considered it was apparent that these smaller fish made relatively large contributions to population-level consumption. Bonus harvest programs focusing on smaller size classes may therefore yield herring mortality reduction, but only if they promote relatively large annual harvests. Although smaller harvests of larger striped bass may provide comparable reductions in herring mortality, elevated harvests of smaller striped bass may be easier to achieve because of their higher vulnerability and desirability to anglers.

Further analyses employing blueback herring population models that incorporate time-variant estimates of natural mortality arising from striped bass predation will be necessary to fully characterize the benefits of the management programs proposed here. Extending our modeling framework to forecast

future blueback herring population states under various striped bass management regimes will require additional information on the relationship between predator/angler foraging behavior and prey/target species abundance. Striped bass typically employ a generalist foraging strategy (Walter et al. 2003) and will therefore opportunistically exploit less desirable but more abundant prey when preferred prey is at low abundance (Chipps and Garvey 2007). Per-capita rates of striped bass consumption rates are therefore likely to be a non-linear function of blueback herring abundance, typified by a "Type 3" functional response (Holling 1959; Beauchamp et al. 2007). Because we measured consumption rates at low levels of prey abundance, they may be underestimates of consumption rate upon recovery of herring populations. Alternatively, it is possible that some size classes of striped bass specializing on river herring prey will consume a constant proportion of the prey population across a wide range of prey abundances (i.e. a "Type 2" functional response). Such a foraging strategy would have depensatory effects on the prey population because striped bass would continue to target and consume blueback herring despite low abundance of herring in the environment (Yodzis 1994). Similarly, angling effort and catch rates for striped bass in the Connecticut River will probably vary with striped bass abundance and management regime (Eggleston et al. 2003; Eggleston et al. 2008). If decreases in striped bass abundance result in declining angling quality, anglers may choose to target striped bass in other locations and/or target other available species in the river. By the same token, a novel opportunity to harvest sub-legal striped bass could produce a "numerical response" (Holling 1959), attracting anglers to the river and intensifying angling pressure.

Our study offers a modest-scale case study of how fishery-dependent data, fishery-independent data and modeling can be integrated to consider management strategies. Regional and range-wide monitoring data had suggested a link between increasing abundance of striped bass and diminishment of blueback herring. We conducted a multiple-year study in the Connecticut River in order to collect targeted data on the interaction. A creel survey of the Connecticut recreational fishery yielded data on patterns of angler catch and harvest as well as striped bass abundance. The availability of these data stimulated discussions of new management approaches, and permitted parameterization of a relatively

simple model designed to assess the efficacy of alternative approaches. Continued local monitoring of the fish species and the recreational fishery will be needed in order to judge whether managing predation through fishery regulations is effective at restoring a species of concern.

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Figures

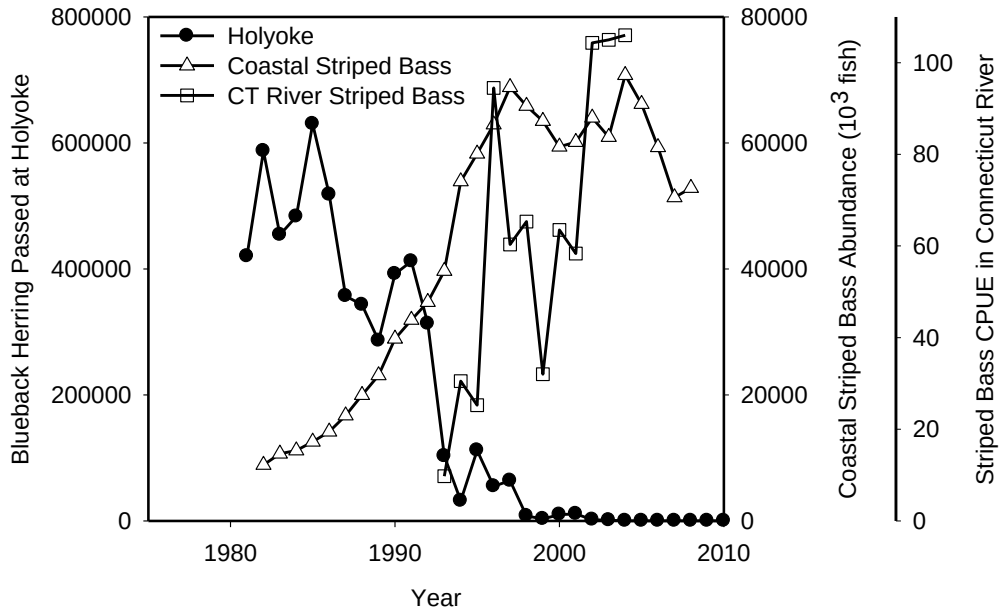

Figure 1 Annual passage of blueback herring at the Holyoke fish elevator during 1981-2010 (USFWS 2011), coastal striped bass abundance (ASMFC 2009; expressed in thousands of fish) during 1982-2008, and striped bass electrofishing catch-per-unit-effort (T. Savoy, unpublished data; unit effort = one electrofishing sample night) at Windsor Locks in the Connecticut River during spring of 1993-2004.

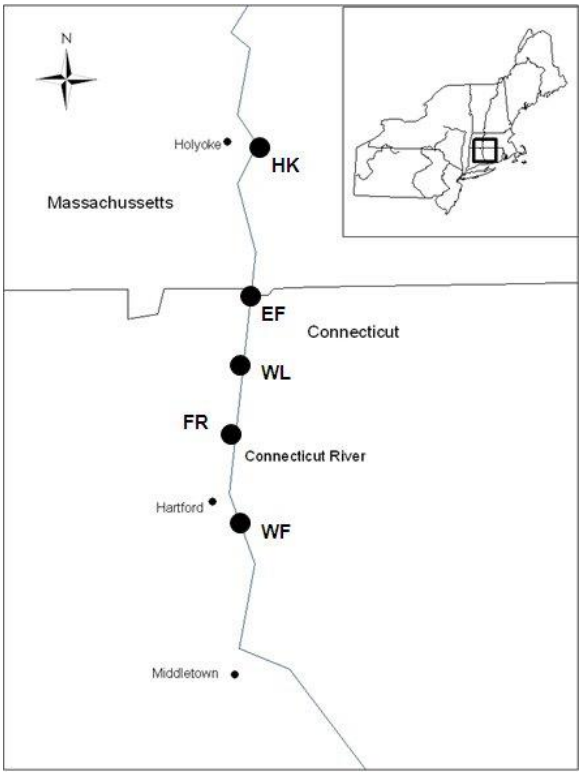

Figure 2 Map of the Connecticut River in Northern Connecticut and Southern Massachusetts. The five sites electrofished in 2005-08 are indicated: WF (Wethersfield), FR (lower Farmington River), WL (Windsor Locks), EF (Enfield), and HK (Holyoke). The 2008 creel survey covered the river segment within Connecticut between Middletown and Enfield.

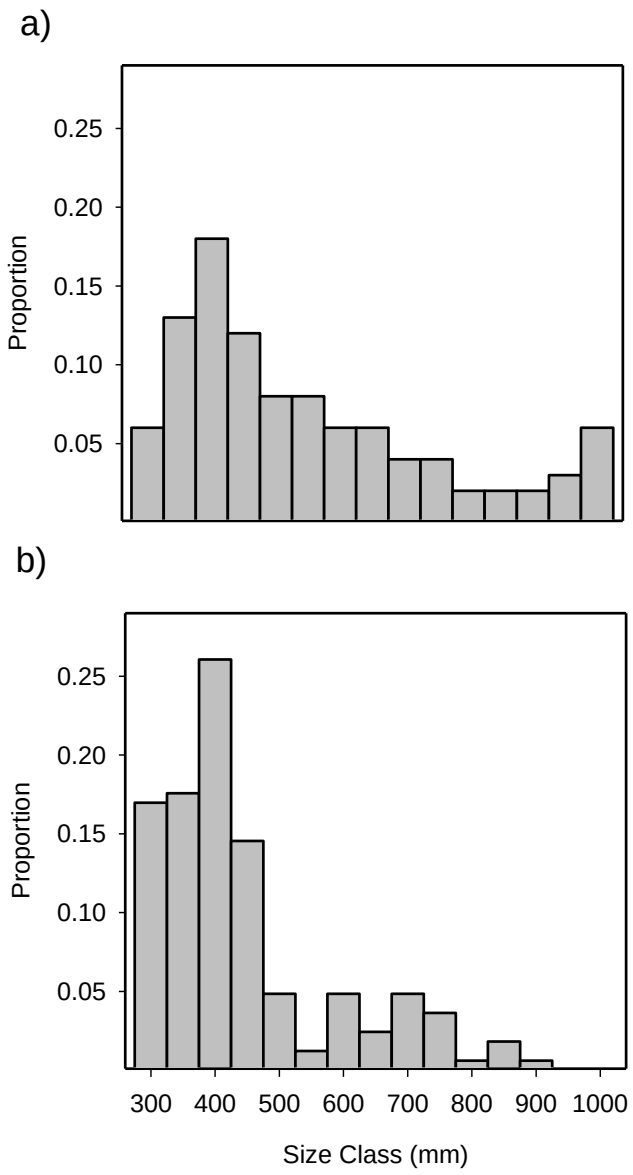

Figure 3 Size structure of striped bass ≥300 mm TL captured in the Connecticut River during the spring migration season. a) Captured via electrofishing during May-June of 2006-07 in the study area (n = 606); b) Captured by recreational anglers during March-June of 2008 in the Connecticut portion of the study area (n = 165 catch events recorded by creel survey interviews).

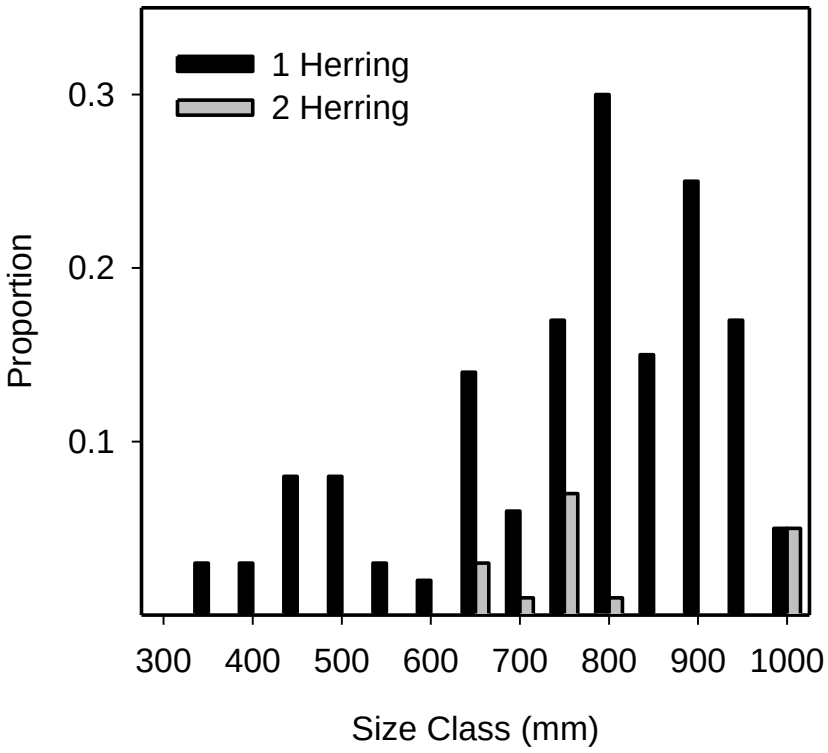

Figure 4 Proportion of striped bass diet samples (n = 642) collected in the study area during May-June of 2005-07 containing one or two herring, presented by 50 mm striped bass size class.

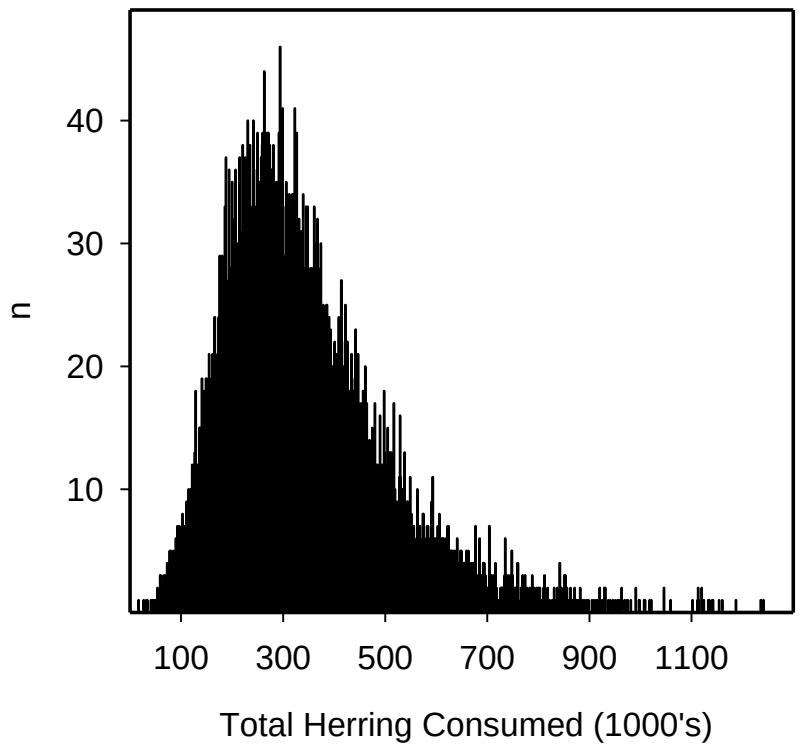

Figure 5 Frequency distribution of population-level blueback herring consumption outcomes from 10,000 iterations of the Monte Carlo consumption model.

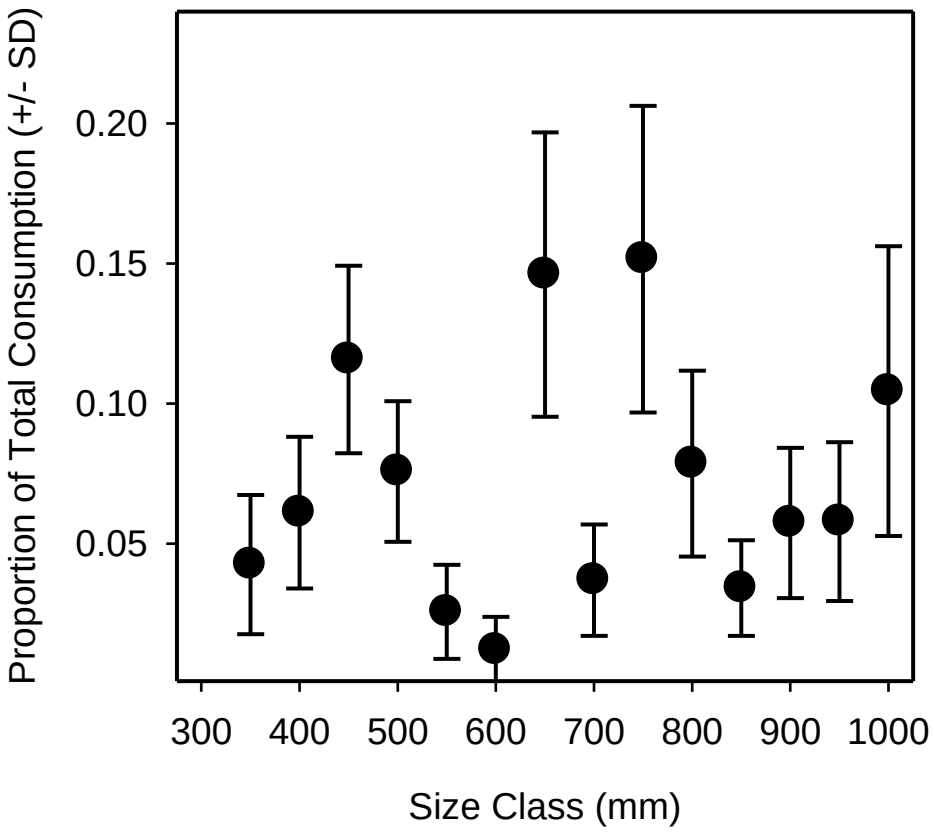

Figure 6 Mean proportion of blueback herring consumption (+/- SD) attributable to each 50 mm striped bass size class in 10,000 runs of the Monte Carlo consumption model.

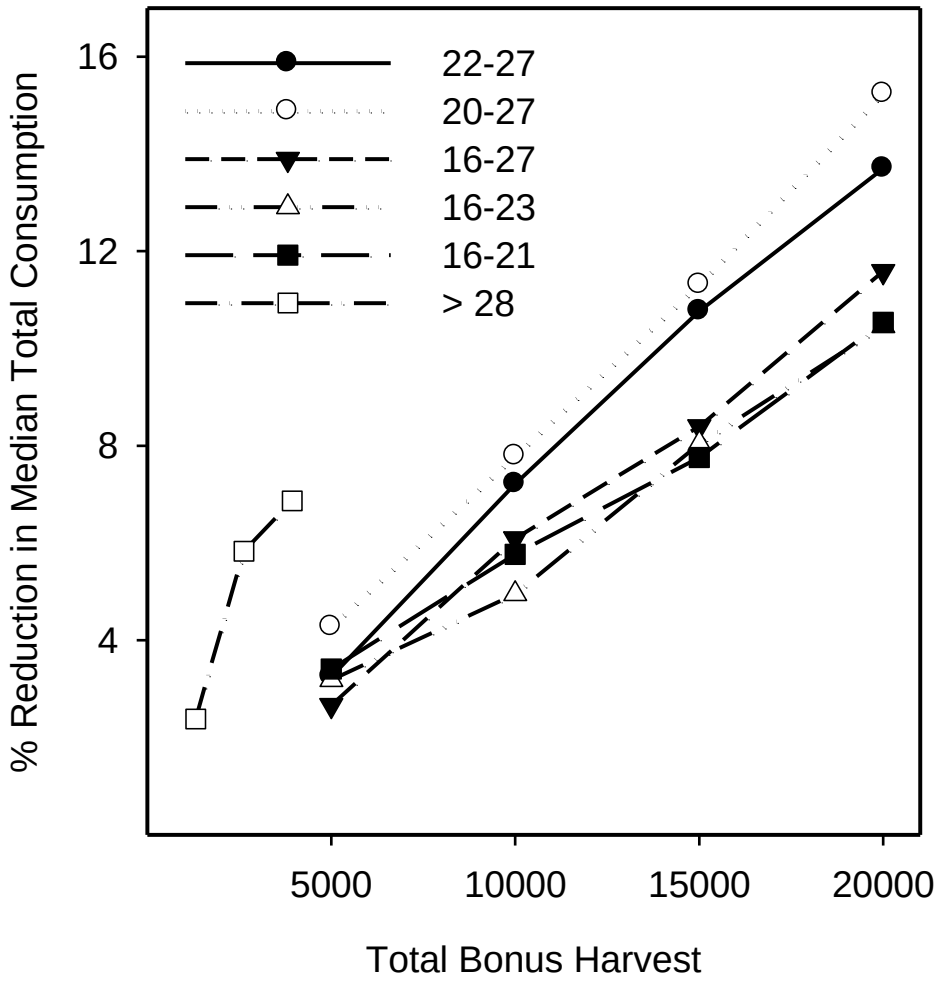

Figure 7 Percent reduction in median total consumption under six alternative "bonus harvest" management scenarios (22-27" slot, 20-27" slot, 16-27" slot, 16-23" slot, 16-21" slot, and increased harvest of fish ≥28") at varying levels of total annual harvest.

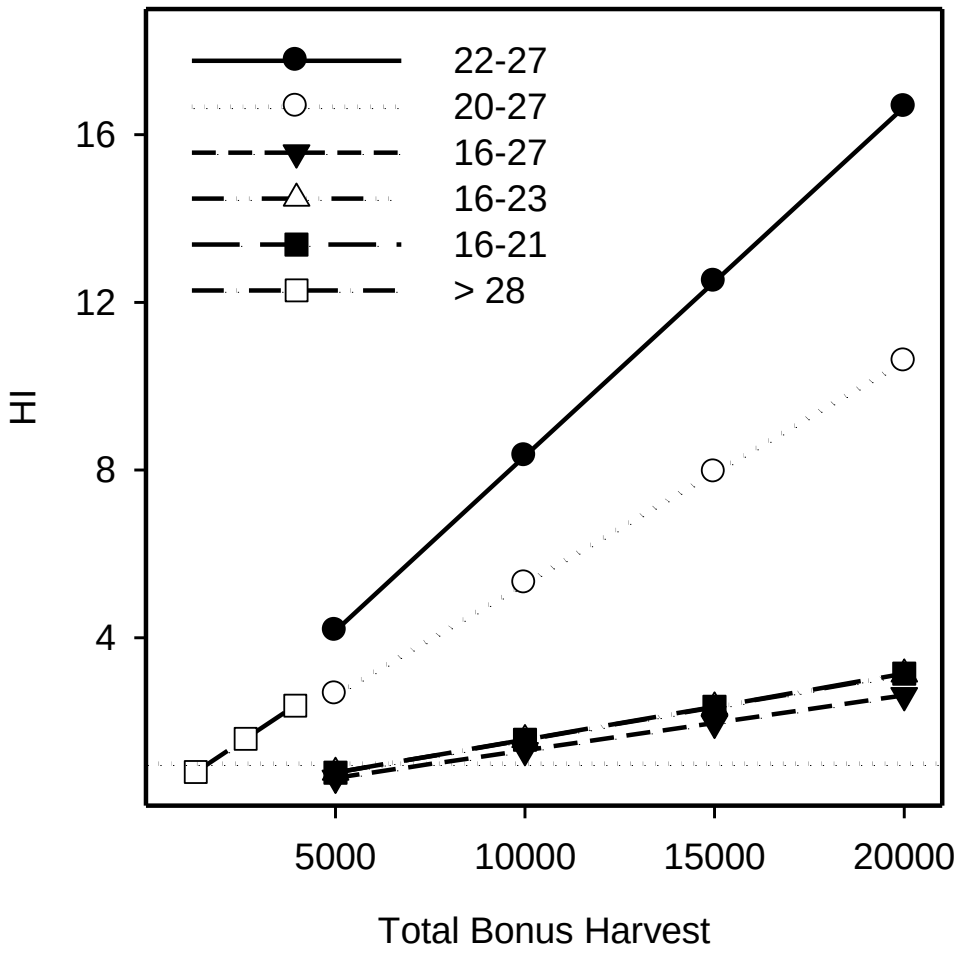

Figure 8 Index of "Harvest Increase" (*HI*), defined as the mean proportion of angler catch of vulnerable striped bass that would have to be harvested based on 2008 creel survey data, for six alternative "bonus harvest" management scenarios (22 – 27" slot, 20 – 27" slot, 16 – 27" slot, 16 – 23" slot, 16 – 21" slot, and increased harvest of fish > 28") at varying levels of total annual harvest. The dotted reference line indicates a value of 1 – i.e. harvest equal to the total catch recorded in 2008.

Chapter 4

Collateral damage of a fishery management success story? Simulation models of the interaction between Striped Bass and Blueback Herring in the Connecticut River.

Abstract

Case studies of the ramifications of predator management for prey population dynamics can play a valuable role in developing ecosystem fisheries management approaches. Atlantic coastal populations of Striped Bass (*Morone saxatilis*), a large predatory finfish of significant fisheries value, have been rebuilt to high levels of abundance in recent decades. The spawning run of Blueback Herring (*Alosa aestivalis*) to the Holyoke Dam on the Connecticut River in Southern New England has collapsed coincident with Striped Bass recovery; our previous study of this predator-prey interaction in the Connecticut River suggested that annual Striped Bass in-river consumption of herring was substantial, and that increased in-river Striped Bass harvests might modestly improve herring survival. Here we incorporate our quantitative measurements of predation rates into a herring population model to test whether increased Striped Bass predatory demand can account for the collapse of the Holyoke Dam run, and whether alternative management of the in-river recreational Striped Bass fishery can substantially improve prospects for run recovery. Over half of our simulations incorporating estimates of Striped Bass predation during the 1980-2000s predicted the observed collapse of the Holyoke run; comparison of these simulations to those without Striped Bass predation suggested substantial reductions in annual egg production, proportions of repeat spawners, and population growth rate arising from Striped Bass predation. Further, current rates of Striped Bass predation in the river stretch below Holyoke Dam appear sufficient to prevent run recovery. Implementation of alternative regulations that encourage increased Striped Bass harvests by recreational anglers offer only limited potential to aid herring recovery; the levels of additional harvest required to substantially improve predicted future herring returns are unlikely to be achieved at observed levels of fishing intensity. Our model illustrates potential trade-offs between predator and prey management initiatives, provides estimates of uncertainty associated with those trade-offs, and highlights important areas for further research into this important predator-prey interaction.

Introduction

Despite a variety of scientific and socio-economic hurdles that have delayed implementation (Pitcher et al. 2009), a number of regulatory bodies are currently poised to operationalize ecosystem-based fisheries management (EBFM). For example, the Atlantic States Marine Fishery Commission (ASMFC) is formulating ecological reference points that may be used to manage the Atlantic Menhaden stock on the U.S. Atlantic coast (SEDAR 2015), and the U.S. National Oceanic & Atmospheric Administration (NOAA) National Marine Fisheries Service (NMFS) recently issued a "road map" for implementation of EBFM for marine fisheries in U.S. federal waters (NOAA 2016). Given that a central focus of EBFM is the explicit incorporation of ecological interactions (Pikitch et al. 2004), studies that quantitatively describe important ecological relationships can aid progress towards EBFM implementation.

Studies of predator-prey interactions can be particularly informative in this regard. Predation is a significant source of mortality for many fish populations that is only indirectly considered in traditional fisheries models (Christensen 1996; Vetter 1988). A proliferation of recent studies has highlighted how fisheries management might be improved by incorporating information on predator-prey interactions (e.g. Bundy and Fanning 2005; Lacroix 2014; Moustahfid et al. 2009; Punt and Butterworth 1995; Temming and Hufnagl 2015). In particular, it has become evident that predator management can have substantial ramifications for prey population dynamics (Ferretti et al. 2010; Shackell et al. 2010). The predictive capability of population models used for management can therefore be improved by incorporating estimates of predation rates; further, assessments of how predator management modulates predation mortality can quantitatively link predator management to prey population dynamics. Modeling prey population dynamics in this context can be viewed as an "ecosystem approach" to management, in which the management focus remains on a managed population or group of populations, but ecological interactions are explicitly considered (Fogarty 2014). An ecosystem approach may be particularly helpful in assessing the trophic implications of top-level predator recovery. Large predatory finfish support many economically and socially significant fisheries, and accordingly, management goals for these species

typically focus on maintaining populations at high abundance. Abundant predators can place high predatory demand on prey populations; this dynamic may create conflicting management imperatives if prey species become imperiled. In the face of this challenge, modeling the linked population dynamics of predator and prey can bring inherent trade-offs into focus and provide a more informed basis for decision-making.

Here we mobilize quantitative measurements of the predator-prey interaction between a recovered predator and an imperiled prey species to illustrate the interplay between predator management and prey conservation. Our focus is the predator-prey interaction between Striped Bass (*Morone saxatilis*) and anadromous Blueback Herring (*Alosa aestivalis*), two sympatric species native to the Atlantic Coast of the U.S. "River herring " (Blueback Herring and closely-related Alewife *A. pseudoharengus*) have declined substantially across much of their range (ASMFC 2012; Hasselman and Limburg 2012), coincident with a successful rebuilding of coastal Striped Bass populations (ASMFC 2015; Richards and Rago 1999). The annual Blueback Herring spawning run to the Holyoke Dam on the Connecticut River in Southern New England crashed from approximately 630,000 fish in the mid-1980s to an average of approximately 250 fish during 2004-14; our study of this spawning run in 2005-07 revealed truncated age structures, reduced rates of iteroparity, and decreased body sizes relative to historic runs, suggesting a state of reduced population resilience (Davis et al. 2009). Prompted by the hypothesis that in-river predation by newly abundant Striped Bass was a major contributor to herring declines (Savoy and Crecco 2004), we surveyed Striped Bass abundance, size structure, and food habits in the Connecticut River in spring 2005-08. Our study documented a large contingent of Striped Bass (>100,000 fish at a mean density approaching 2,000 fish/river km) that was capable of consuming 200,000-800,000 Blueback Herring annually (Davis et al. 2012), a significant predatory loss in light of annual herring passage at Holyoke Dam in recent years. Using our estimates of Striped Bass demography and consumption rates, coupled with data on the in-river recreational fishery for Striped Bass (Davis et al. 2011), we estimated that increased Striped Bass harvests under a variety of alternative management scenarios could reduce annual Blueback Herring predatory losses by 4-10% (Davis et al. 2012).

The analyses presented in Davis et al. (2012) provided a first step towards understanding the ramifications of Striped Bass management for Blueback Herring in the Connecticut River, but did not fully address two important questions: a) whether increased in-river Striped Bass predation during the 1980-2000s could quantitatively account for the crash of the Blueback Herring run to Holyoke Dam during the 1990-2000s, and b) whether alternative management of the in-river recreational fishery for Striped Bass could facilitate Blueback Herring recovery. In this study, we use a structured population model, informed by our measurements of the predatory-prey interaction between Striped Bass and Blueback Herring as well as of the recreational fishery for Striped Bass, to address these questions. The specific objectives of this study were to 1) construct and parameterize a stage-structured population model of the "above-Holyoke" Blueback Herring population (i.e. considering the segment of the Connecticut River Blueback Herring run spawning above Holyoke Dam as a distinct population); 2) incorporate estimates of Striped Bass predation and resulting predation mortality into the model; 3) incorporate estimates of Striped Bass removals and attendant reductions in predation mortality that might be achieved under a variety of alternative management scenarios into the model; 4) conduct model simulations with and without Striped Bass predation (assuming status quo management of the Striped Bass in-river fishery) to assess the relative contribution of Striped Bass predation to the crash of Blueback Herring at Holyoke Dam during the 1990-2000s; and 5) conduct model simulations incorporating Striped Bass predation and alternative in-river management scenarios to assess potential benefits to herring conservation.

Methods

Model Construction

We constructed a simple stage-structured, discrete time model of the Blueback Herring population spawning above Holyoke Dam (Fig. 1). The model divided the population into eight stages: age 1-5 immature fish, and age-aggregated mature fish that have spawned in 0, 1 or 2 previous years. Abundances at each stage in model year *t* were defined as,

$I_{a,t} = \sum_b \left(M_{b,t-1}/2\right) F_b S_{J,t}$; if a=1, b=0, 1, 2 (1)

$$= I_{1,t-1} S_I \text{ ; if } a=2 \quad (2)$$

$$= I_{a-1,t-1} S_I (1 - B_a) \text{ ; if } a=3, 4, 5 \quad (3)$$

$$M_{b,t} = \left(\sum_a I_{a,t-1}\, S_I B_{a+1}\right) + I_{5,t-1} S_I \text{ ; if } b=0, a=2, 3, 4 \quad (4)$$

$$= M_{b-1,t-1} S_M \text{ ; if } b=1, 2 \quad (5)$$

where a=age in years; b=number of years in which mature fish previously spawned; I_a=immature fish of age a; M_b=mature fish that have spawned in b previous years; F_b=fecundity; S_J, S_I, and S_M=annual survival of age-0, immature, and mature fish, respectively; and B_a=probability that immature fish mature at age a. The model makes the following assumptions: a) sex ratios of mature fish are equal; b) no straying occurs; c) all fish mature by age 6; d) mature fish do not "skip" spawning years; e) survival of mature and immature fish is independent of age or size; and f) fish spawn a maximum of three times (stage M_2 is terminal).

We parameterized the model using information from a survey of the Blueback Herring and Striped Bass populations in the "upper" Connecticut River (uppermost 64 river km, from Wethersfield, CT to the Holyoke Dam, of the 139 river km between the river mouth and the dam) during spring 2005-08 (Davis et al. 2009; Davis et al. 2012), from a creel survey of the Striped Bass fishery in the upper Connecticut River in spring 2008 (Davis et al. 2011; Davis et al. 2012), and from the literature. Model simulations projected the population over a 50 year period beginning in the year 1982, a year which roughly corresponds with peak abundance of Blueback Herring at Holyoke Dam, and is also the first year for which estimates of coastal Striped Bass abundance are available (ASMFC 2015). The specific methods used to parameterize the model and conduct simulation analyses are described below. An inventory of model inputs and parameters can be found in Appendix 1. All analyses were performed in SAS v. 9.4.

Survival Rates

We used the method of Hoenig (1983) to estimate annual survival of immature herring (S_I=0.61) at sea (assuming natural mortality only), using a maximum age of nine years (ASMFC 1990). We

estimated annual survival of mature herring during the 1980-90s (S_M=0.33) using demographic data reported by Marcy (1969) for Blueback Herring in the Connecticut and nearby Thames River in 1966-67, as well as annual mortality rates reported for Blueback Herring in the Charles and Monument Rivers in Massachusetts during 1985-1993 (ASMFC 2012). Given that these survival rates were measured during a period of low coastal (and presumably in-river) Striped Bass abundance, we considered them indicative of mature fish survival in the absence of in-river Striped Bass predation. We also estimated annual survival of mature herring in the presence of in-river Striped Bass predation using 2005-07 demographic data from the upper Connecticut River (Davis et al. 2009); these rates were used to estimate the proportion of herring consumed in the upper Connecticut River that originated from the above-Holyoke population (see *Striped Bass Consumption*).

Absent any measurements of juvenile survival rates in the Connecticut River, we used the method outlined by Bailey and Zydlewski (2013) to estimate juvenile survival as a density-dependent function of egg production. Juvenile survival in model year *t* was estimated using a Ricker (1975) stock-recruitment relationship,

$$S_{J,t} = \left[\alpha O_t e^{-\beta(O_t)}\right]/O_t \quad (6)$$

where O_t=total egg production $\left(\sum_b \left(M_{b,t-1}/2\right)F_b\right)$, and α and β are the shape parameters of the stock-recruitment relationship. The density-independent parameter α was set such that the intrinsic spawning run growth rate (*r*) was 0.4, an intermediate level for river herring runs (ASMFC 1990). The value of α producing the desired level of *r* was estimated by running a series of deterministic simulations using the "base model" (see *Simulation Analyses*) in which: a) initial spawning run size was set to 5,000 fish; b) β was set to zero (i.e. eliminating density-dependence); c) α for each simulation was set to a fixed value between .0001-.0005; and d) all other model parameters were fixed at their deterministic values (Appendix 1). For each simulation, we estimated *r* as the exponential annual increase in run size; we then regressed α on *r* across simulations to find α when *r*=0.4 ($\alpha=2.4\text{x}10^{-4}$). We then conducted simulations with α set to $2.4\text{x}10^{-4}$ and β set to a fixed value between $1\text{x}10^{-11}$ to $9\text{x}10^{-11}$. For each of these simulations,

the run size asymptote *k* (i.e. run size at which, in the absence of stochasticity, density-dependence prevented further appreciable annual increases in run size) was estimated as the mean run size over the last 25 years of the simulation. We then regressed *k* on β and solved for β that yielded $k=2x10^6$ ($\beta=3.3x10^{-11}$), based on an estimated 7,900 acres of spawning habitat available above the Holyoke Dam (CRASC 2003) and the State of Maine's management goal of 235 adult herring returns per acre of spawning habitat (ASMFC 2012).

Mean Length, Fecundity, Maturity Probabilities

We estimated fecundity at various mature fish stages as a function of body size (total length or TL). We used demographic data reported from Marcy (1969) and the upper Connecticut River during 2005-08 (Davis et al. 2009) to estimate historic and contemporary mean lengths (mm) of mature herring. To incorporate likely reductions in reproductive potential of the population arising from decadal demographic shifts (Davis et al. 2009), all model simulations used historic mean lengths for the years 1982-2004 and 2005-08 mean lengths for years 2005 and later.

We used recent estimates of fecundity from a Southern New England river herring run to estimate fecundity of Blueback Herring in the Connecticut River. Ganias et al. (2015) conservatively estimated that anadromous Alewives spawning in Bride Brook in Connecticut spawned 780 eggs per gram of gonad-free body mass during the spawning season. We regressed natural log-transformed gonad-free body mass (g) vs. natural log-transformed total length (mm) for female Blueback Herring (n=468) collected from the upper Connecticut River during 2005-08, and the resulting equation [$\log_e(\text{mass})=-8.74+2.5(\log_e(\text{length}))$; $R^2 = 0.78$] was used to estimate gonad-free body mass at the mean length of each mature herring stage. Estimated gonad-free body masses were then multiplied by 780 to estimate fecundities.

Maturity probabilities for ages 3-5 were estimated from those reported for four anadromous Alewife populations in the Canadian Maritime Provinces (Gibson 2004) and for the Monument River in Massachusetts (ASMFC 2012). The maturity probability at a given age was estimated as the mean of reported maturity probabilities for that age.

Striped Bass Consumption

We incorporated Striped Bass predation into "full models" (see *Simulation Analyses*) by estimating predatory losses in each model year using data on Striped Bass abundance, size structure, and food habits obtained from the upper Connecticut River during 2005-08 (Davis et al. 2012), as well as estimates of Striped Bass size structure in the upper Connecticut River during 1993-2004 (T. Savoy, unpublished data). The total number of herring from the above-Holyoke population consumed in the upper Connecticut River in model year *t* was estimated as,

$$C_t = H\left[V \sum_i \left(n_{i,t} q_{i,1}\right) + 2\left(n_{i,t} q_{i,2}\right) \right] ; \; i = 30, 35, 40 \ldots . \geq 100 \qquad (7)$$

where *H*=the proportion of total herring consumed in the upper Connecticut River that were part of the above-Holyoke population (see below for estimation procedure); *V*=the number of days in the spring migration season; n_i=the abundance of Striped Bass in 50-mm size class *i*; and $q_{i,1}$ and $q_{i,2}$ are proportions of Striped Bass in size class *i* that consumed one or two Blueback Herring daily (Davis et al. 2012). The length of the spring migration season was based on observed durations of Striped Bass and Blueback Herring residence in the upper Connecticut River during 2005-08.

To estimate the abundance of Striped Bass in each size class, we first estimated the absolute abundance of Striped Bass ≥30 cm TL in the upper Connecticut River in model year *t* as,

$$SB_{CT\ River,t} = \left(SB_{CT\ River,2008} / SB_{Coastal,2008}\right) SB_{Coastal,t} \qquad (8)$$

where $SB_{CT\ River,\ 2008}$=absolute abundance of Striped Bass ≥30 cm TL in the upper Connecticut River in 2008=1.2×10^5 fish (Davis et al. 2012); $SB_{Coastal,\ 2008}$=estimated abundance of the Atlantic coast Striped Bass stock in 2008=1.6×10^8 fish (ASMFC 2015); and $SB_{Coastal,\ t}$=estimated abundance of the Atlantic coast Striped Bass stock (ASMFC 2015). For model years beyond 2014 (most recent year for which estimate of coastal abundance is available), $SB_{CT\ River,\ t}$ was estimated using $SB_{Coastal,\ 2014}$ (ASMFC 2015). Striped Bass abundance by size class in each model year was estimated using size structure data obtained from the upper Connecticut River in spring 1993-2004 (T. Savoy, unpublished data) and 2006-07 (Davis et al.

2012). Proportions-at-length from 1993 were used to estimate n_i for model years 1982-1992; a mean of 2006-07 proportions-at-length were used for model years 2005 and later.

We estimated annual survival of mature fish in full models by considering predation during the relatively brief vernal migration as analogous to a "Type 1" fishery (Ricker 1975). Accordingly, we treated the fraction of the "above-Holyoke" spawning run consumed by Striped Bass in each model year $\left(C_t / \sum_b M_{b,t}\right)$ as the "exploitation rate" and (1-S_M) as the conditional mortality rate for mature fish surviving Striped Bass predation. Annual survival of mature fish in full model year *t* was therefore calculated as

$$S_{M,SB,t} = 1 - \left(C_t / \sum_b M_{b,t} + \left((1 - S_M)\left(1 - \left(C_t / \sum_b M_{b,t}\right)\right)\right)\right) \quad (9)$$

If the estimated exploitation rate was greater than 0.99 for any model year then it was manually set to 0.99. We substituted $S_{M,SB,t}$ for S_M in equation 5 for all full model simulations. We also assumed that all female herring consumed in a given model year made no contribution to egg production in that year; accordingly, we made the following adjustment to equation 1 for all full model simulations:

$$I_{a,t} = \sum_b \left(M_{b,t-1}/2\right)\left(C_t / \sum_b M_{b,t}\right) F_b S_{J,t} \text{ ; } a=1,\ b=0,\ 1,\ 2 \quad (10)$$

If application of the exploitation rate to abundance resulted in fewer than 10 fish in any stage, then M_b was manually set to 10 fish.

Because Striped Bass in the upper Connecticut River likely consume herring that are not part of the above-Holyoke population, we adjusted our consumption estimates by a proportional correction factor (*H*, equation 7). To estimate *H*, we conducted a series of full model simulations, with all parameters other than *H* fixed at their deterministic values; *H* was set to a fixed value ranging from 0.05 to 1 in each simulation. From each simulation, we calculated mean $S_{M,SB}$ for years 2005-07. We then regressed *H* on $S_{M,SB}$ and solved for *H* that yielded $S_{M,SB}$=0.24 (*H*=0.71), the mean estimated mature fish survival rate during 2005-07.

Alternative Management Scenarios

We conducted a series of model simulations to explore changes in Blueback Herring population trajectories that might be achieved through alternative management of the Striped Bass recreational fishery in the upper Connecticut River. These "bonus harvest" simulations used the full model, with the addition of annual bonus harvests of Striped Bass (i.e. harvests in addition to those assumed to occur under prevailing length and creel limits) for model years 2000 and later (see *Simulation Analyses*). The annual harvest of Striped Bass from each vulnerable size class under a given bonus harvest scenario in model year *t* was estimated as,

$$h_{i,t} = B(Y_i / \sum_i Y_i) \quad (11)$$

where B=total annual bonus harvest of Striped Bass and Y_i=estimated angler catch of Striped Bass from size class *i* in the upper Connecticut River during spring 2008 (Davis et al. 2011; Davis et al. 2012). We expanded estimates of Striped Bass catch from the 2008 angler survey (which surveyed the portion of the upper Connecticut River between Wethersfield and the Connecticut/Massachusetts border) to the entire upper Connecticut River by dividing by 0.65 (creel survey area=41.8 river km, upper Connecticut River=64.4 river km). We assumed that all Striped Bass harvested as part of the bonus harvest made no contribution to annual herring consumption; accordingly, for all bonus harvest simulations, we subtracted h_i from n_i in equation 7 for all vulnerable size classes. To assess the feasibility of achieving various levels of *B*, we calculated the mean proportion of vulnerable Striped Bass that would have to be harvested and the ratio of estimated harvest to observed angler catches in 2008 ($\sum_i h_{i,t} / \sum_i n_{i,t}$ and $\sum_i h_{i,t} / \sum_i Y_{i,t}$, respectively, for all vulnerable size classes) in each model year.

Stochasticity

Stochasticity was incorporated into all simulations by randomly selecting model parameters from appropriate distributions in each model year. Mature (S_M) and immature (S_I) survival, maturity probabilities (B_a), and the consumption correction factor H were randomized by drawing samples of *n* from binomial distributions parameterized with deterministic values for each parameter, with *n* for each

randomization set to a value that produced the desired range of randomized output (Appendix 1). Fecundity (F_b) at each mature stage was randomized by selecting a normal variable from a distribution parameterized with the mean and standard deviation of observed length-at-stage, then using this randomized length value to estimate fecundity. To incorporate stochasticity in juvenile survival ($S_{J,t}$), we fit a Ricker stock-recruitment curve to the annual Connecticut River Blueback Herring juvenile abundance index (Benway 2015) for years in which at least 10,000 Blueback Herring passed above Holyoke Dam, treating annual passage above Holyoke as the predictor and the juvenile abundance index (geometric mean catch per seine haul) as the response. We expressed residuals from this relationship as a proportion of the predicted value and calculated a standard deviation (σ_R) of proportional residuals. We then adjusted equation 6 to incorporate stochastic recruitment,

$$S_{J,t} = \left[\alpha O_t e^{-\beta(O_t)} + \left[R_t\left[\alpha O_t e^{-\beta(O_t)}\right]\right]\right]/O_t \qquad (12)$$

where R_t=a normal variable drawn from a distribution with mean=0 and standard deviation=σ_R. If the randomized value of R_t in any model year was less than -0.95 then it was manually set to -0.95.

For full models, we randomized $SB_{CT\ River,t}$ by drawing the number of recaptures used to calculate $SB_{CT\ River,2008}$ from a poisson distribution with mean=19 (number of 2008 tag recaptures; see Davis et al. 2012). Size structure (proportions-at-length) was randomized by sampling the number of Striped Bass ≥30 cm TL measured in each year from a multinomial distribution parameterized with observed proportions-at-length. Proportions of Striped Bass in each size class consuming 0-2 herring per day were randomized by sampling the number of Striped Bass lavaged in each size class in 2005-07 from a multinomial distribution parameterized with the observed proportions of Striped Bass that consumed 0-2 herring (Davis et al. 2012). The number of days in the spring migration season was randomized by sampling integers between 30 and 50 from a uniform distribution (Davis et al. 2012).

For bonus harvest simulations, we randomized harvest from each vulnerable size class (h_i) by drawing B samples from a multinomial distribution parameterized with observed proportions of angler catch per vulnerable size class in 2008.

Simulation Analyses

We conducted analyses to assess the contribution of Striped Bass predation to declines in the above-Holyoke Blueback Herring population, and the potential to mitigate herring declines via alternative management of the recreational fishery for Striped Bass in the upper Connecticut River:

1) 100 stochastic "base model" simulations that did not incorporate Striped Bass predation. The results of this analysis served as a comparative baseline for subsequent analyses.
2) 100 stochastic "full model" simulations incorporating Striped Bass predation.
3) 100 stochastic "bonus harvest" simulations, utilizing the full model from the previous analysis, with the addition of a "bonus harvest" fishery instituted in the year 2000 (year of onset of persistent low annual herring returns to the Holyoke Dam). We conducted bonus harvest simulations under a variety of alternative management scenarios (see below).

All simulations lasted for 50 years, corresponding to the years 1982-2031. For all simulations, the initial abundances in each stage were determined by setting $I_{1,t}$ to a range of values, and then calculating the resulting abundance of all subsequent stages using deterministic transition probabilities (e.g. $I_{2,t} = S_I I_{1,t}$, $I_{3,t} = S_I I_{2,t}(1-B_3)$, etc.); we selected a value of $I_{1,t}$ at which initial run size ($\sum_b M_{b,1}$) was equal to 650,000 fish (the approximate peak run size at Holyoke in the 1980s), which produced a spawning run consisting of 31% repeat spawners in model year 1. Five bonus harvest slot limit scenarios targeting sublegal size classes were modeled: 22-27 in (40-69 cm), 20-27 in (51-69 cm), 16-27 in (40-69 cm), 16-23 in (40-58 cm), and 16-21 in (40-53 cm). The annual harvest (B) under each slot limit was varied from 5,000 to 20,000 fish in increments of 5,000 (i.e. 4x100 bonus harvest simulations under each slot limit scenario; 20x100 total bonus slot limit simulations). We also modeled alternative management scenarios predicated on bonus harvests of legal-sized Striped Bass (≥28 in or 71 cm); in this case B was varied from 2-4 times the estimated harvest of legal-sized Striped Bass from the upper Connecticut River in spring 2008 (n=2,020 fish).

For each simulation, we assessed spawning run size ($\sum_b M_{b,50}$) and proportion of repeat spawners $\left[\left(M_{1,50} + M_{2,50}\right)/\sum_b M_{b,50}\right]$ in the final simulation year (t_{final}=50), total egg production (O_t) in each model year, and the stochastic run size growth rate (Morris and Doak 2002),

$$\lambda_s = \left[\sum_t log_e\left(\sum_b M_{b,t+1}/\sum_b M_{b,t}\right)\right]/t_{final}\ ;\ t=1,2\ldots t_{final}\text{-}1 \qquad (13)$$

For full model and bonus harvest simulations, we also assessed Striped Bass consumption (C_t) and the resulting exploitation rate $\left(C_t/\sum_b M_{b,t}\right)$ in each model year. The spawning run was considered to have "crashed" in any simulation in which spawning run size in the final simulation year=30 fish (i.e. 3x the minimum abundance in any mature fish stage, see equation 10). For each analysis type, we estimated the proportion of simulations in which the spawning run crashed and used Chi-Square tests to test for differences in proportions of runs that crashed under various modeling scenarios.

Sensitivity Analysis

We assessed the sensitivity of final run size ($\sum_b M_{b,50}$) in a deterministic full model simulation to immature (S_I) and mature (S_M) survival rates, maturity probabilities (B_3, B_4, B_5), mean length-at-stage for mature fish, eggs spawned per gram of gonad-free body mass, the parameters of the stock-recruitment curve (α and β), initial abundances in each model stage, striped bass consumption rates, number of days in the migration season (V), consumption correction factor (H), and Striped Bass abundance ($SB_{CT\ River}$) and size structure. Changes in final run size were evaluated after a 1% increase in each parameter. Sensitivity was defined as the absolute value of percent change in final run size; final run size was considered "highly sensitive" to all parameters for which sensitivity was greater than 1% (Bailey and Zydlewski 2013; Haefner 2005). We assessed sensitivity to Striped Bass consumption rate by increasing both consumption proportions ($q_{i,1}$ and $q_{i,2}$) for each size class by 1%. The number of days in the migration season was increased by 1% from its midpoint (V=40). To assess sensitivity to Striped Bass size structure, we adjusted n_{800} for each model year by 1%, as this size class had the highest observed incidence (31%) of herring consumption in 2005-07; to offset increases in n_{800} (i.e. to hold overall Striped

Bass abundance constant), we decremented n_{300} as this size class of Striped Bass did not consume herring in 2005-07.

Results

Impact of Striped Bass Predation

Full model simulations suggest Striped Bass predation was a major source of mortality for the Blueback Herring in the upper Connecticut River during the 1990-2000s coincident with the crash of the spawning run to the Holyoke Dam. Base model simulations – i.e. those that projected herring population trajectories in the absence of Striped Bass predation – predicted a median run size of 1.9×10^6 fish in the final model year, with zero simulations predicting a run crash (Fig. 2). In contrast, 53% of full model simulations predicted a run crash by the final model year, with 25% of simulations predicting a crash by the year 2000. Median run size in base models rose to approx. 2.0×10^6 fish (i.e. *k*) by 1995 and then subsequently oscillated near this upper limit, whereas median run size in full models declined dramatically beginning in 1993 (roughly coincident with the observed onset of declines at Holyoke) and crashed by 2018 (Fig. 2). Median predicted Striped Bass consumption in the full model rose through the early 1990s, peaking at approx. 800,000 herring in 1997 (interval between 5th and 95th percentiles i.e. 90% CI=400,000-1.5×10^6) before gradually declining to approx. 300,000 fish annually by the end of the simulation period (Fig. 3). Accordingly, the median estimated fraction of the above-Holyoke run consumed annually by Striped Bass ("exploitation rate"; see equation 9) rose markedly during the 1990-2000s, reaching approx. 0.82 by 2005 (Fig. 3). Based on median exploitation rate, the full model predicted that Striped Bass were capable of consuming 90-100% of the spawning run to Holyoke Dam from 2012 onwards (Fig. 3). The substantial impact of Striped Bass predation on the above-Holyoke Blueback Herring population was evident in all output metrics: the median final run size in base models approximated the 90th percentile of full models ($\approx 1.9 \times 10^6$ fish), final proportions of repeat spawners were generally lower in full models (5th percentile base model≈25th percentile full model≈0.16), median egg production among model years was 65% lower in full models, and population growth rate was negative in approximately half of full model years, a condition that never occurred in base models (Fig. 4).

Alternative Management Scenarios

The alternative management scenarios we modeled for the Striped Bass fishery in the upper Connecticut River offered limited potential for conserving Blueback Herring, and the required levels of additional harvest are unlikely to be achieved given the observed intensity of the recreational fishery. Median run size in the final model year was >30 (i.e. >50% of runs did not crash) in most bonus harvest simulations employing a bonus slot scenario and B>10,000 (Fig. 5). Bonus harvest simulations assuming harvests of 20,000 fish from slots focused on larger fish (20-27 in and 22-27 in) predicted the largest median final run sizes, approaching the 75th percentile of full model simulations (Fig. 5); however, final run sizes produced by these slot limit simulations vs. those produced by full model simulations were not substantially different based upon the high degree of overlap in predicted final run sizes. Relative to full model simulations, proportions of runs that did not crash were higher in all bonus slot limit scenarios assuming bonus harvests of 15,000 or 20,000 fish, and in all scenarios assuming tripling and quadrupling harvest of legal-sized fish (Fig. 6), although proportions of non-crashed runs in bonus harvest vs. full model simulations were significantly different in only one instance (B=20,000: 22-27 in vs. full p=0.02; 20-27 in vs. full was only marginally insignificant, p=0.06). However, bonus harvest scenarios that predicted the greatest improvements in herring population trajectories would likely require prohibitively large angler harvests. For instance, a harvest of 15,000-20,000, 22-27 in Striped Bass represents 70-95% of available fish (Fig. 7-A), or 9-11 times the observed catch in that size range (Fig. 7-B). More moderate levels of proportional harvest would be required under legal harvest scenarios (22-32% of available fish; see Fig. 7-A), but anglers would still have to harvest approximately double the number of legal-sized fish caught (Fig. 7-B). Bonus harvest regulations that appear to be more feasible (e.g. harvesting 5,000-10,000 Striped Bass from a 16-23 in slot limit; see Fig. 7) offer little apparent conservation benefit for Blueback Herring (Fig. 5-6).

Sensitivity Analysis

Run sizes in the final model year of full model simulations were highly sensitive to immature survival (S_I: sensitivity=3.5), and the parameters of the stock-recruitment relationship (α: sensitivity=12.0;

β=1.3; see Table 1). Final run size was also moderately sensitive to mature survival (S_M: sensitivity=1.0). Sensitivity values for most other inputs and parameters ranged from 0.1 to 0.3 (Table 1).

Discussion

Model simulations incorporating estimates of in-river predation during the 1980-2000s suggest that recovery of coastal Striped Bass stocks made a substantial contribution to the collapse of the Blueback Herring run to Holyoke Dam on the Connecticut River. By the mid-1990s, we estimate that Striped Bass consumed as many as 1.5 million adult herring annually in the upper Connecticut River during the vernal migration season; as a result, median predicted run size at Holyoke declined markedly during the 1990s, with 25% of simulations predicting run collapse by the year 2000. By the mid-2000s, simulations predicted that Striped Bass annually consumed 80% of the adult herring originating from the "above-Holyoke" population that migrated to the upper river; by the end of the 50-year simulation period, predatory losses rose to 90-100% of the run to the upper river. Additional harvests of Striped Bass by recreational anglers may offer some potential for improving herring survival, but will require annual harvests on the order of 15,000-20,000 Striped Bass from larger size classes (20-27") of sub-legal bass – an outcome that seems improbable at current levels of fishing effort.

Our median model projections declined in a manner similar to observed declines in run size at the Holyoke Dam during the 1980-90s; however there were some notable differences between absolute values of model projections and observed Holyoke run sizes. Full model simulations predicted higher run sizes during the 1980s-early 1990s than were observed at Holyoke (e.g. median predicted run size in 1990 was 1.4×10^6 fish vs. an observed run size of 390,000 at Holyoke), predicted a less pronounced decline during the 1990s (decline in median predicted run size from 1990 to 2000=68%; Holyoke run decline=98%), and predicted higher run sizes throughout the 2000s than were observed at Holyoke (average median run size 2004-14=169,000 fish; Holyoke average run size=250). It is apparent that our model over-predicts run size. Over-predicted run sizes in early model years could be attributable to inflated estimates of abundance-at-stage in the first model year, and may also be attributable to

overestimation of the carrying capacity of habitat above Holyoke Dam (i.e. *k*), although this latter explanation seems implausible give the substantial amount of habitat available above the dam (≈8,000 acres) and substantially higher estimates of carrying capacity made by other authors (≈$8x10^6$ herring; see CRASC 2003). The model's propensity to over-predict run size in later model years could reflect inflated estimates of juvenile or immature survival; absent empirical information, we relied largely on information from the literature to estimate these quantities, and model predictions were particularly sensitive to these two parameters. Year class strength is thought to be determined during the first year of life for anadromous alosines (Crecco et al. 1986; Crecco and Savoy 1985; Crecco and Savoy 1987). Therefore, empirical data on early life history stages for this population could improve the predictive capability of our model. Additionally, our assumption of no straying from the above-Holyoke population – that herring born below the dam would not migrate above the dam as adults, and that herring born above the dam would not select a spawning site below it – is likely unrealistic. Although anadromous alosines are known to display relatively high rates of fidelity to natal rivers (Gahagan et al. 2012; Havey 1961; Jessop 1994; Melvin et al. 1986; Turner 2015), substantial straying within natal rivers has been observed (Messieh 1977). It is probable that herring born above Holyoke Dam, upon returning to the river as mature adults, may spawn below the dam if environmental conditions are not favorable for extended upstream migration, or if intense predation in the upper river discourages migration to the dam. If such within-river straying is common and is biased towards downstream spawning, than our model as currently constructed will over-predict run size at Holyoke. Collection of information on within-river fidelity rates and the mechanisms governing extent of upstream migration represents another avenue for improving the predictive capability of our model.

Our model also made necessary simplifications that should be considered when making inferences from simulation results. With respect to model structure, our model was not truly age-structured (mature fish stages were age-aggregated), and also limited the number of lifetime spawning events to three although blueback herring have been observed to spawn up to five times in their lifetime at

northern latitudes (Loesch 1987; Marcy 1969). Faced with a relatively data-poor situation, we chose to simplify model structure and therefore minimize error arising from over-parameterization (Fogarty 2014); a necessary tradeoff was that our model did not directly allow for the possibility of truncated age structures, which could have substantial ramifications for population growth and resiliency (Davis and Schultz 2009), and also had limited range to evince declines in iteroparity (which likely explains why of output metrics examined, proportions of repeat spawners showed the least pronounced variation in base vs. full models; see Fig. 4). Therefore, our model likely over-estimated the resiliency of the blueback herring run (potentially contributing to over-prediction of run size discussed above); this condition suggests that Striped Bass predation may be an even greater stressor than indicated by our simulation analyses. When estimating Striped Bass predation, we a) assumed Striped Bass in-river abundance was a time-invariant function of coastal abundance, and based this relationship on observed in-river and coastal abundances in 2008; b) assumed that Striped Bass abundance and size structure would remain relatively constant during the 2000s, and c) assumed that Striped Bass consumption rates (as measured in 2005-07) were time-invariant and not density-dependent – i.e. they did not vary as a function of prey density. We speculate that our approach under-estimates Striped Bass consumption during the 1980-90s. We measured Striped Bass consumption rates during a period (mid-2000s) of relatively low in-river herring abundance; it is probable that Striped Bass consumption rates were higher in years when herring prey were more readily available – particularly if Striped Bass employed a generalist feeding strategy typified by a "Type 3" functional response (Holling 1959) which predicts increases in predator per-capita consumption rates with increases in abundance of preferred prey items. Similarly, we measured Striped Bass in-river abundance in 2008, when coastal abundance had decreased somewhat from the peaks observed during the 1990s. We conjecture that higher coastal abundances during the 1990s likely created greater competition for coastal prey resources, and therefore greater impetus for Striped Bass to undertake potentially costly (in energetic and physiological terms) migrations above the head of tide in coastal rivers to exploit secondary prey resources. The larger herring runs to the upper Connecticut River during the 1990s also likely created a more attractive feeding opportunity for coastal Striped Bass, increasing the fraction of the

coastal stock that migrated to the upper river. The probability that our estimates of in-river Striped Bass consumption during the 1980-90s were conservative, yet still of a sufficient magnitude to cause herring run collapse in a majority of model simulations, further underscores the substantial role that Striped Bass predation likely played in the decline of the Holyoke spawning run. We view our assumption that Striped Bass abundance and size structure during the 2000s remained relatively constant as reasonable, given that it is in keeping with prevailing management policy for coastal Striped Bass stocks, which seeks to maintain the population at a relatively high and stable biomass, and seeks to maintain a size structure featuring abundant legal-sized (>28 in or 71 cm) fish (ASMFC 2015).

Our simulations suggest that Striped Bass predatory demand in the upper Connecticut River is currently sufficient to prevent recovery of the Holyoke run. Upon initial consideration, it seems counterintuitive that large numbers of Striped Bass would continue to migrate to the upper river given the apparent collapse of the feeding opportunity provided by the above-Holyoke herring population. However, we estimated well over 100,000 Striped Bass present in the upper Connecticut River in 2008 (Davis et al. 2012), a year in which only 84 herring passed Holyoke Dam (USFWS 2015). Blueback Herring in our downstream study sites (Wethersfield and lower Farmington River) were generally an order of magnitude more abundant than at upstream sites in 2005-07 (Davis et al. 2009). Spawning aggregations of Blueback Herring in these downstream areas likely provide a feeding opportunity sufficient to attract large numbers of Striped Bass to the upper Connecticut River, and may therefore be indirectly suppressing recovery of the above-Holyoke population. If in-river predation by Striped Bass continues to hold the above-Holyoke population at severely depleted abundances, depensation, or a decrease in per-capita population growth rate arising from factors such as difficulty in finding a mate, may further complicate population recovery (Frank and Brickman 2000; Shelton and Healey 1999). In the absence of a substantial reduction in the Striped Bass contingent in the upper river effected either directly through the in-river recreational fishery or indirectly through reductions in coastal Striped Bass abundance, it is not clear what management actions might improve prospects for recovery of the Holyoke

herring run. Current efforts to "trap and truck" river herring from downstream areas to habitat above the Holyoke Dam (Sprankle 2015) may provide one avenue of overcoming the Striped Bass predation "bottleneck" (given that Striped Bass rarely migrate above the dam) , although this management approach may produce short-term gains in population abundance at the cost of population genetic integrity and long-term evolutionary potential (Hasselman and Limburg 2012).

Our study suggests that Striped Bass predation is an important stressor for Connecticut River Blueback Herring, but it is not clear that Striped Bass predation is a ubiquitous stressor for coastal river herring populations. In Southern New England, where Blueback Herring declines have been most pronounced (Palkovacs et al. 2014), incidence of river herring in Striped Bass diets during marine residence are relatively limited (Nelson et al. 2003). Bioenergetic studies have suggested that Striped Bass in estuarine residence may consume substantial numbers of juvenile alosines (Hartman 2003; Hartman and Brandt 1995), but the recent shifts towards maturation at younger ages and smaller sizes that have been observed in many river herring populations (ASMFC 2012; Davis and Schultz 2009; Palkovacs et al. 2014) are symptomatic of elevated mortality during adult, not juvenile life history stages (Conover et al. 2005; Reznick and Ghalambor 2005). We conjecture that Striped Bass may most effectively exert substantial predatory pressure on Blueback Herring populations when the two species are concentrated together during vernal migrations into large coastal rivers. This brief but intense interaction can, as our case study demonstrates, have outsized implications for river herring population dynamics; however, it is necessarily constrained to those systems that can accommodate substantial contingents of Striped Bass. River herring abundance and demography have changed substantially in systems range-wide, many of them too small to accommodate in-river Striped Bass migration (e.g. Davis and Schultz 2009). The ubiquity of river herring declines range-wide across a variety of systems points to common stressors most likely operating in the marine environment, e.g. bycatch in marine fisheries (Cournane et al. 2013; Hasselman et al. 2016) or oceanic warming (Lynch et al. 2014). Striped Bass predation may therefore be a

substantial stressor operating in concert with other stressors for some populations, and a negligible stressor for other populations.

Simulations of herring population trajectories under alternative Striped Bass in-river management scenarios suggest that increased Striped Bass harvests in the Connecticut River may have potential to aid Blueback Herring recovery, yet the harvest levels necessary to achieve substantial reductions in predatory losses may be difficult to achieve given the observed intensity of the recreational fishery in the upper river during 2008. However, the spring fishery for Striped Bass in the Connecticut River is prosecuted along the entire river below Holyoke, and is particularly intense near the mouth of the river (Davis et al. 2011). It is possible that anglers fishing throughout the river may be able to more readily achieve additional harvests on the order of 20,000 fish annually (although given a lack of information on Striped Bass movements within the river, it is not clear if removal of Striped Bass in downstream areas will translate into reductions in Striped Bass abundance in the upper river). Institution of a bonus harvest program may also attract increased angler participation in the fishery. The Connecticut Department of Energy and Environmental Protection (CDEEP) instituted a Striped Bass "bonus harvest" program in 2011 (Davis et al. 2012), initially limited to the Connecticut River but later expanded to all state waters, that allowed anglers to harvest approximately 5,000 sub-legal Striped Bass annually (the program utilized Connecticut's commercial quota allocation which in previous years had gone unfilled as commercial harvest of Striped Bass is prohibited in Connecticut). This program has proved to be highly popular with anglers, who have enthusiastically embraced the opportunity to harvest smaller Striped Bass; these smaller fish generally contain lower levels of contaminants such as PCBs and mercury, are more readily caught by anglers, and are viewed by many as more palatable (D. Simpson, CDEEP, personal communication). Finally, our estimates of the plausibility of achieving modeled harvest are based on a single year of creel survey data. Inter-annual variability in angler effort and catch may be considerable in an environment such as the upper Connecticut River where environmental conditions (e.g. spring river flows and precipitation) that play a role in angler success vary considerably from year. Overall, increased

harvest of Striped Bass from the upper river may offer real potential for improving river herring recovery prospects and may be more readily achievable than suggested here.

Increasing in-river harvests of Striped Bass in the Connecticut River with the goal of improving survivorship of an imperiled prey species illustrates the potential conflicts and tradeoffs inherent to adoption of an ecosystem approach to management. Recently, daily bag limits for the coastal Striped Bass recreational fishery were reduced (from two to one fish) because of concerns that overfishing of the coastal Striped Bass stock was occurring (ASMFC 2015). Relaxed harvest regulations for Striped Bass in the Connecticut River, despite offering potential benefits for river herring conservation, run counter to the current coast-wide goal of reducing Striped Bass harvests. However, considerable effort and money has been invested in restoring Blueback Herring to the upper Connecticut River, and this population is part of a regional genetic stock that has suffered particularly acute declines (Palkovacs et al. 2014); increased harvests of Striped Bass may therefore be warranted if such an action offers potential river herring conservation benefits. A modeling approach such as ours can inform debate over modifying Striped Bass management to conserve river herring by illustrating potential trade-offs (e.g. our results suggest that removing 20,000 22-27 in Striped Bass from the Connecticut River, or approximately .01% of the coastal stock, would increase median annual herring egg production by an order of magnitude), providing estimates of uncertainty around those trade-offs (the 90% CI for annual egg production in the previous example is $1.8x10^{6}$-$1.3x10^{11}$ eggs), and highlighting important areas where additional data would improve predictive capability (e.g. survival of immature fish at sea). Our model is relatively simple and relies on the types of information readily generated by management agency surveys (e.g. electrofishing and creel surveys), and may therefore be more readily adopted and implemented in management decision-making than complex ecosystem models with high data demands (Fogarty 2014). Ultimately, case studies such as ours can provide incremental improvements in understanding of ecosystem structure and function, and therefore can serve as valuable "building blocks" in EBFM development.

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Tables

Table 1 Sensitivity of run size in the final model year of deterministic full model simulations to a 1% change in various inputs and parameters. Sensitivity was defined as the absolute value of percent change in final run size (e.g. a 1% change in immature survival produced a 3.45% change in final run size).

Parameter	Sensitivity
Immature Survival (S_I)	3.5
Mature Survival (S_M)	1.0
Age 3 Maturity Probability (B_3)	0.2
Age 4 Maturity Probability (B_4)	0.3
Age 5 Maturity Probability (B_5)	0.1
Mean Length of Mature Fish Stages	0.2
Eggs per Gram Gonad-Free Mass	0.1
Stock-Recruitment Curve: α	12.0
Stock-Recruitment Curve: β	1.3
Initial Abundances	0.0001
Consumption Rate ($q_{i,1}$ and $q_{i,2}$)	0.3
Migration Season Length (V)	0.03
Consumption Correction Factor (H)	0.3
Striped Bass Abundance ($SB_{CT\ River}$)	0.3
Striped Bass Size Structure (n_{800})	0.02

Figures

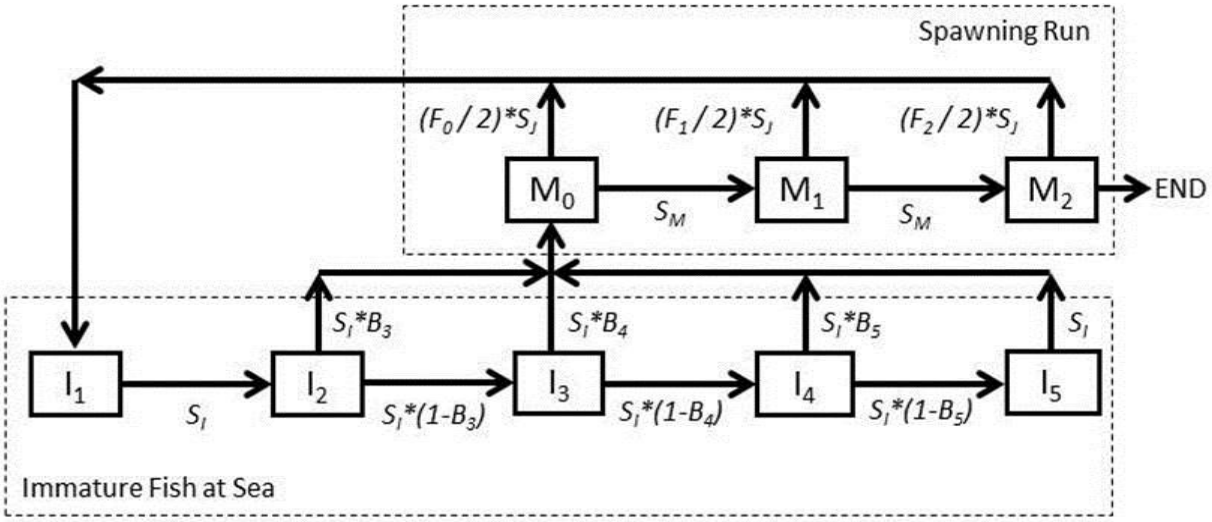

Figure 1 Schematic of the stage-structured model of the "above-Holyoke" Connecticut River blueback population. The population is divided into age 1-5 immature fish at sea (I_1-I_5), and mature fish that have spawned 0-2 times previously (M_0-M_2; stage M_2 is the terminal stage of the model). Transition probabilities from each stage are shown, and are defined by: annual survival rates of juvenile age-0 (S_J), immature (S_I), and mature (S_M) fish; maturity probabilities at age 3-5 (B_3-B_5; assumed maturity probability at age 6=1); and fecundity of mature fish that have spawned 0-2 times previously (F_0-F_2; assumed sex ratio of mature fish=1:1).

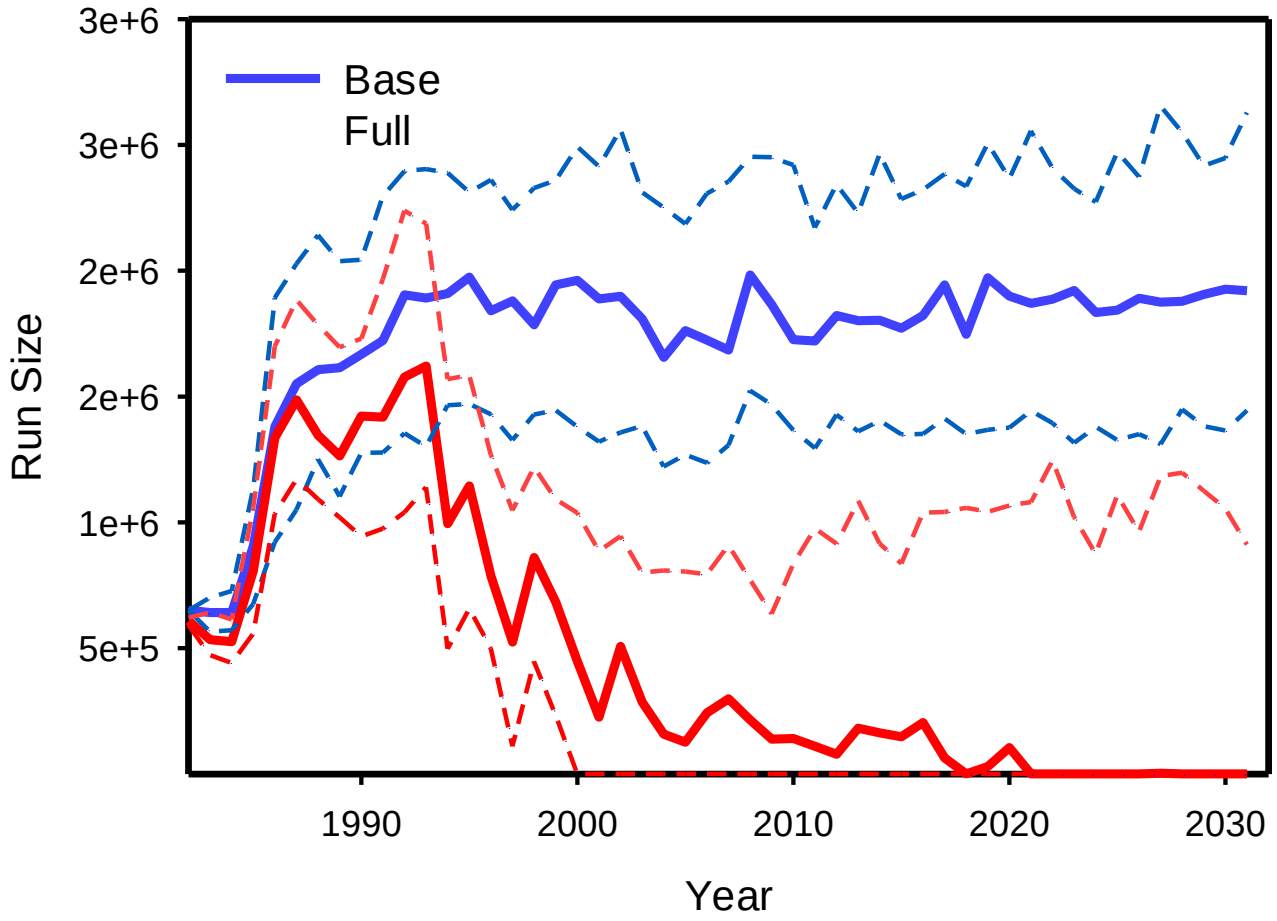

Figure 2 Median run size by model year from 100 simulations using the base (no Striped Bass predation) and full (including Striped Bass predation) models. Dashed lines indicate 25th and 75th percentiles of run size.

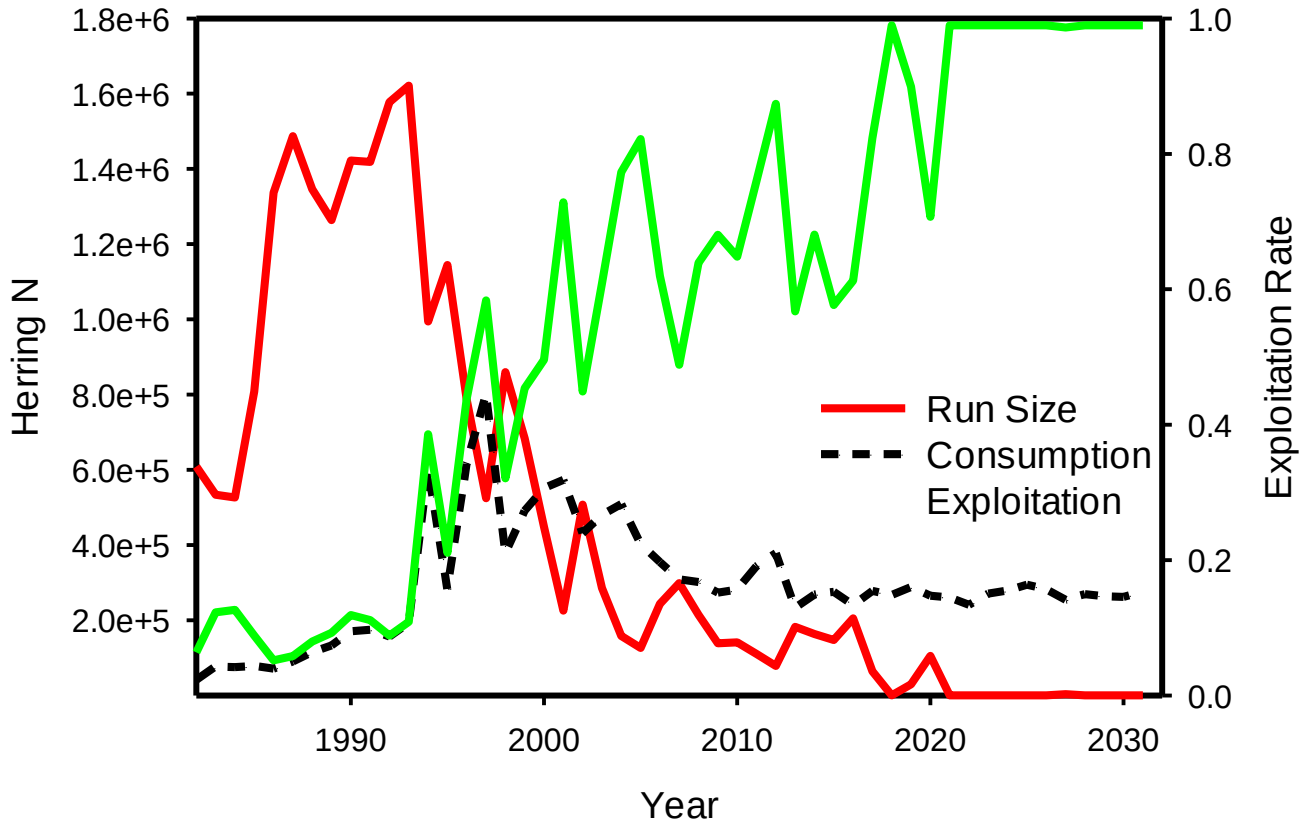

Figure 3 Median run size (escapement from Striped Bass consumption), median potential consumption of herring in-river annually by Striped Bass, and median exploitation rate (i.e. fraction of above-Holyoke run that did not escape Striped Bass predation) by model year from 100 simulations of the full model.

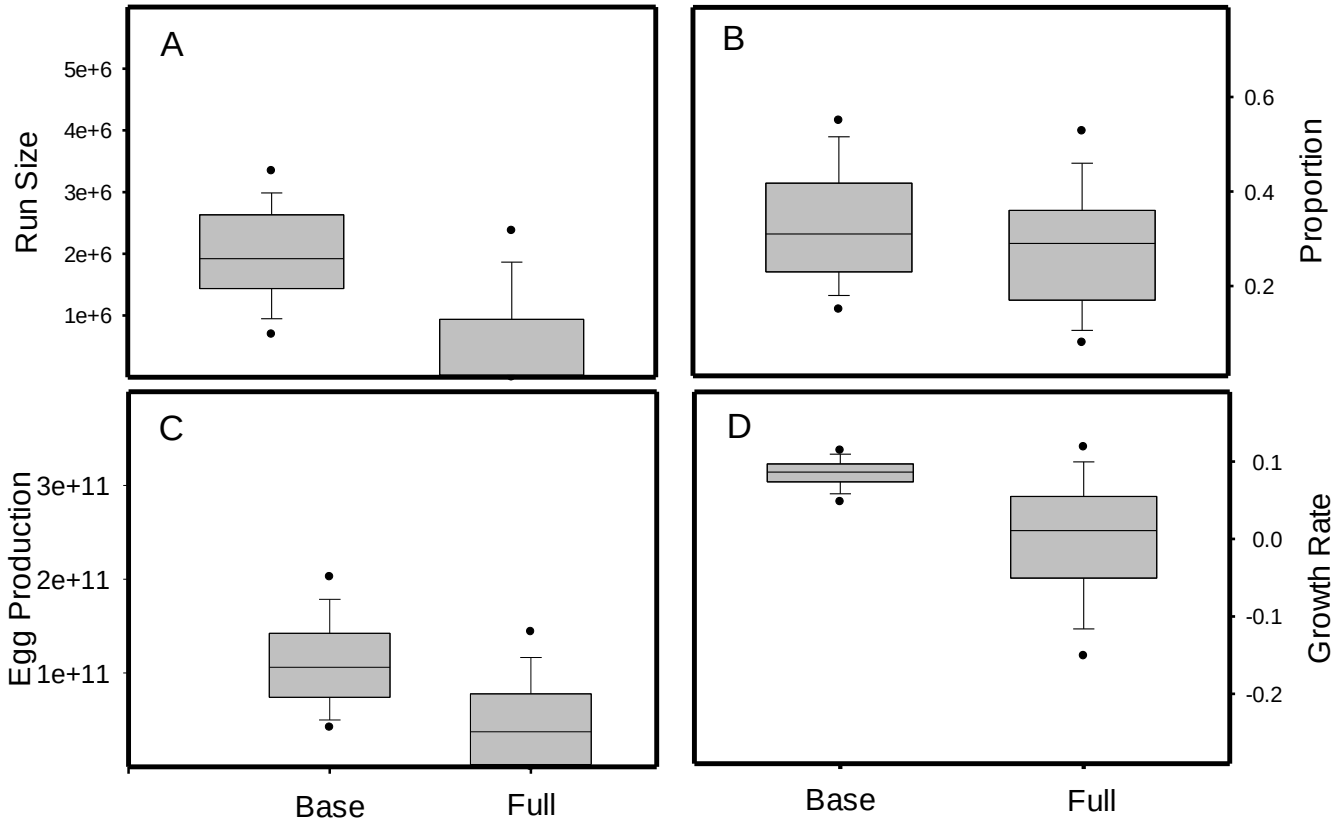

Figure 4 Distributions of run sizes (A) and proportions of repeat spawners (B) in final model years, total egg production in each model year (C), and mean stochastic run size growth growth rate (D) from 100 simulations using the base (no Striped Bass predation) and full (including Striped Bass predation) models. Boxes indicate range between 25th and 75th percentiles, vertical bars within boxes indicate medians, error bars indicate 10th and 90th percentiles, dots indicate 5th and 95th percentiles.

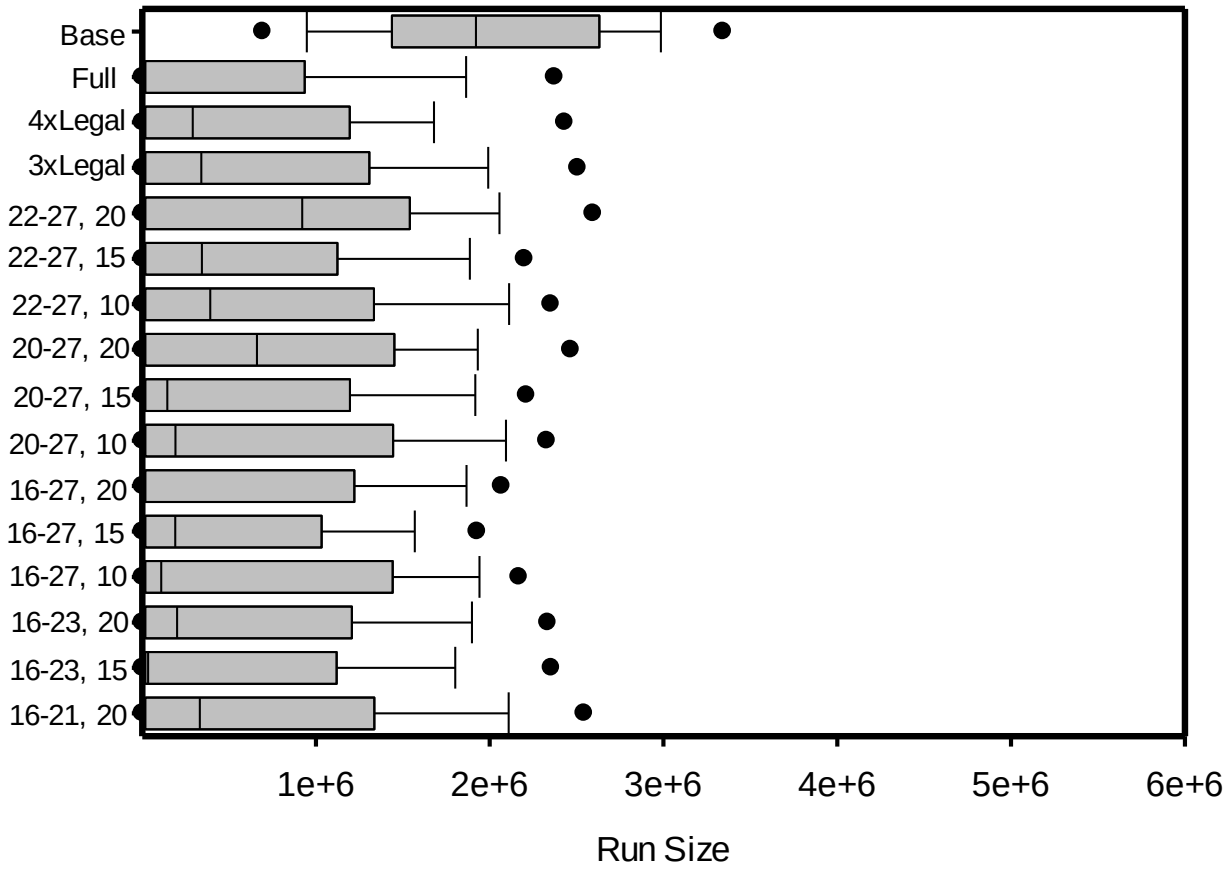

Figure 5 Distributions of run sizes in the final model years of base model, full model, and bonus harvest simulations. Bonus slot scenarios are labeled with the harvest slot size range (inches), followed by the level of bonus harvest (thousands of fish). Boxes indicate range between 25th and 75th percentiles, vertical bars within boxes indicate medians, error bars indicate 10th and 90th percentiles, dots indicate 5th and 95th percentiles. Excludes nine scenarios in which median final run size=30 (i.e. >50% of runs crashed).

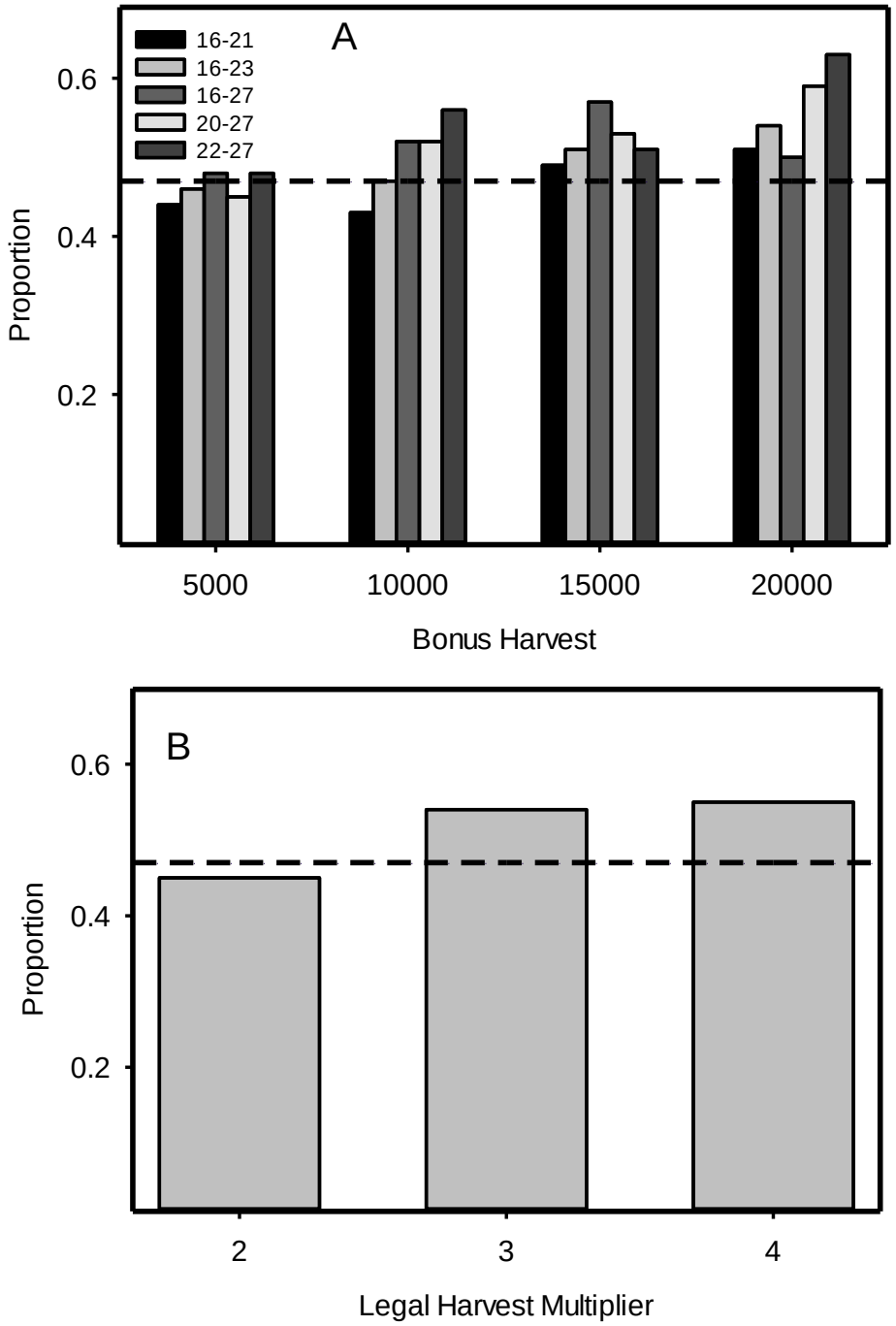

Figure 6 Proportions of runs that did not crash during 100 bonus harvest simulations conducted under bonus slot (A) and increased legal harvest (B) scenarios. Dashed line indicates the proportion of runs that did not crash in 100 full model simulations (0.47).

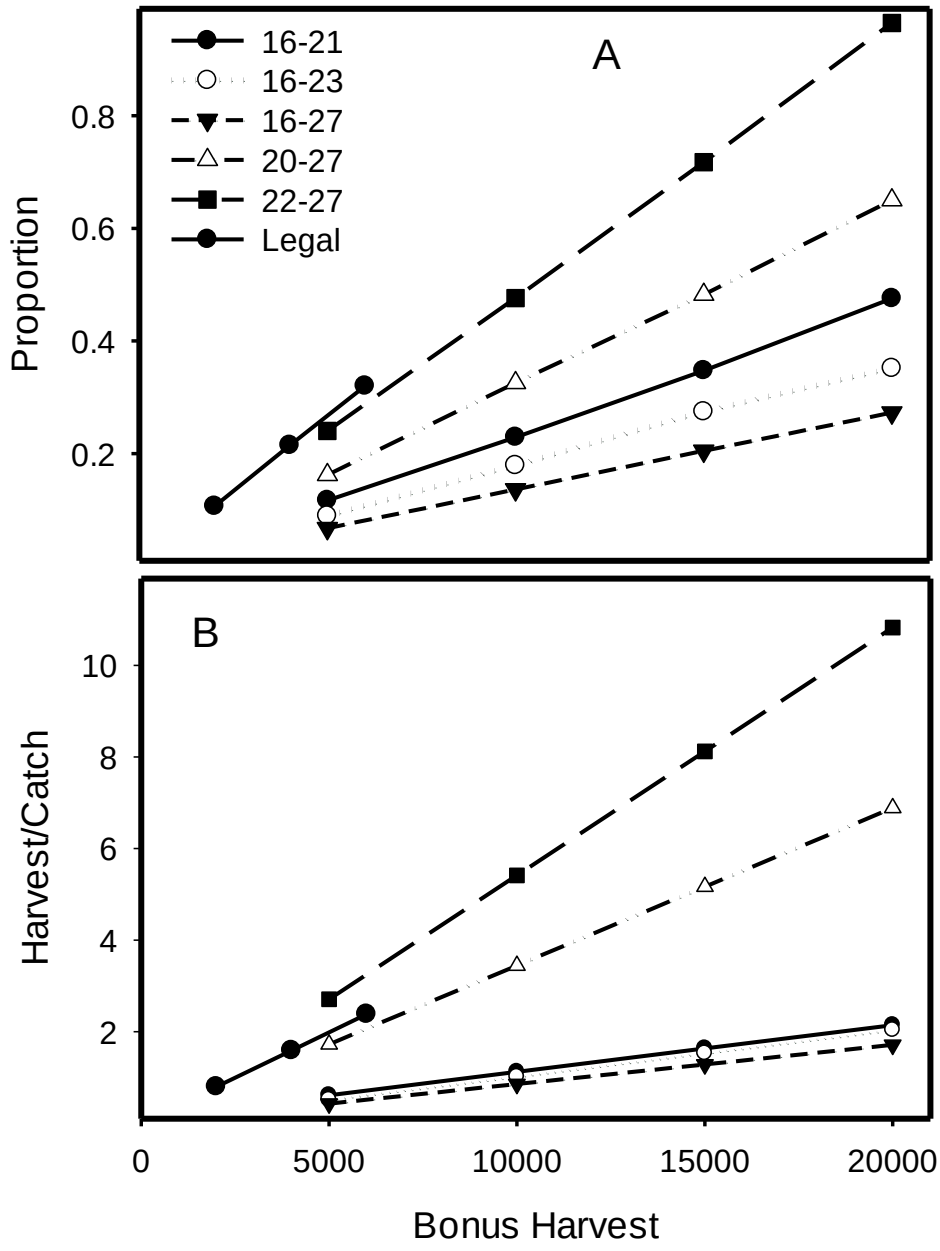

Figure 7 Proportion of available Striped Bass in vulnerable size classes that would need to be harvested under bonus harvest scenarios (A), and ratio of harvest from vulnerable size classes under bonus harvest scenarios to observed angler catch in vulnerable size classes in 2008 (B).

Appendix 1. Parameters and inputs used for model simulations.

Table A1-1 Annual survival rates, maturity probabilities, mean lengths (TL, mm) of mature fish stages, consumption correction factor, fecundities, and stock-recruitment curve parameters. Values in the "Deterministic" column are the point estimates derived from pertinent data or literature (see Methods for details). The column "Stochastic" describes how inputs or parameters were randomized for stochastic model simulations (lack of entry in this column indicates that a particular input or parameter was not randomized for stochastic simulations, with the exception of fecundity, which was randomized via randomizing the mean length input). For inputs or parameters that were randomized, the "Observed Range" column indicates the range of that input or parameter in the data or literature used to estimate deterministic values; the column "Stochastic 90% CI" indicates a 90% confidence interval or CI for randomized values (based on 5th and 95th percentiles of 1,000 randomly-generated values).

Parameter	Deterministic	Stochastic	Observed Range	Stochastic 90% CI
S_I	0.61	Binomial(S_I,n); n=70	None[1]	0.51-0.71
S_M	0.33	Binomial(S_M,n); n=30	0.20-0.50	0.20-0.47
B_3	0.22	Binomial(B_3,n); n=20	0.10-0.50	0.10-0.40
B_4	0.75	Binomial(B_4,n); n=10	0.50-1.00	0.50-1.00
B_5	0.94	Binomial(B_5,n); n=10	0.80-1.00	0.80-1.00
Mean Length M_0, historic	274	Normal(274,σ); σ=9.1	244-321[2]	259-288
Mean Length M_0, contemporary	254	Normal(254,σ); σ=17.5	206-303[3]	225-283
Mean Length M_1, historic	292	Normal(292,σ); σ=9.4	248-320[2]	276-307
Mean Length M_1, contemporary	278	Normal(278,σ); σ=12.0	247-310[3]	259-298
Mean Length M_2, historic	304	Normal(304,σ); σ=10.6	245-330[2]	274-308
Mean Length M_2, contemporary	292	Normal(292,σ); σ=7.7	254-306[3]	265-291
H	0.71	Binomial(H,n); n=10	0.28-1.00[4]	0.50-0.90
F_0, historic	127,223			
F_0, contemporary	105,223			
F_1, historic	149,201			
F_1, contemporary	132,124			
F_2, historic	165,144			
F_2, contemporary	148,574			
α	2.4×10^{-4}			
β	3.31×10^{-11}			
σ_R	0.57			
[1]=no range available, set randomization to produce 90% CI of +/- .10 of deterministic estimate				

Table A1-1 (*continued*)

[2]=based on minimum and maximum lengths reported for ages at which fish had spawned *b* times, with *b*≥2 aggregated; Marcy (1969) did not explicitly report length ranges for fish based on previous spawning frequency
[3]=*b*≥2 aggregated
[4]=based on range of 0.19-0.31 for mature fish survival rate calculated from 2005-07 data

Table A1-2 Abundances in each model stage in model year 1 for initial run size=650,000 fish (all analysis simulations) and initial run size=5,000 fish (stock-recruitment curve fitting).

Stage	Run Size=650,000	Run Size=5,000
$I_{1,1}$	1,874,310	14,417
$I_{2,1}$	1,143,329	8,794
$I_{3,1}$	543,996	4,184
$I_{4,1}$	82,959	638
$I_{5,1}$	3,036	23
$M_{0,1}$	451,734	3,475
$M_{1,1}$	149,072	1,147

Table A1-3 Striped Bass proportions-at-length by 50-cm sizeclass in the upper Connecticut River during 1993-2004 (T.Savoy, unpublished data) and during 2006-07 (Davis et al. 2012; mean of 2006-07). The SAS randomization procedure used to generate stochastic proportions-at-length could not accept proportions=0 and required all proportions-at-length to sum to 1. In some years, no fish were measured in some size classes and/or proportions-at-length did not sum to 1 due to rounding errors. To address these issues where necessary, all year/size class for which proportion-at-length=0 were set to .0001, and then the entry in the most abundant (i.e. greatest proportion-at-length) size class in that year was adjusted until proportions-at-length summed to 1 for that year.

Size Class (cm)	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2006-07
30	0.304	0.05	0.447	0.16	0.06	0.13	0.05	0.03	0.10	0.06	0.02	0.03	0.06
35	0.10	0.178	0.19	0.08	0.04	0.03	0.13	0.04	0.05	0.17	0.06	0.06	0.13
40	0.16	0.06	0.02	0.12	0.06	0.10	0.16	0.02	0.05	0.32	0.14	0.11	0.18
45	0.001	0.02	0.08	0.05	0.03	0.11	0.11	0.07	0.07	0.08	0.169	0.10	0.12
50	0.13	0.001	0.001	0.04	0.07	0.04	0.05	0.13	0.05	0.03	0.15	0.11	0.08
55	0.06	0.05	0.02	0.03	0.06	0.11	0.05	0.13	0.10	0.02	0.06	0.20	0.08
60	0.06	0.11	0.02	0.05	0.08	0.13	0.03	0.07	0.12	0.03	0.02	0.12	0.06
65	0.06	0.06	0.001	0.03	0.12	0.139	0.12	0.03	0.07	0.03	0.04	0.05	0.06
70	0.06	0.11	0.06	0.04	0.14	0.13	0.08	0.09	0.06	0.02	0.05	0.04	0.04

Table A1-3 (*continued*)

75	0.06	0.08	0.04	0.11	0.08	0.02	0.06	0.11	0.05	0.04	0.10	0.02	0.04
80	0.001	0.03	0.04	0.09	0.09	0.02	0.06	0.09	0.10	0.04	0.08	0.07	0.02
85	0.001	0.001	0.04	0.07	0.07	0.02	0.02	0.04	0.11	0.07	0.05	0.03	0.02
90	0.001	0.11	0.02	0.05	0.04	0.001	0.02	0.06	0.05	0.03	0.03	0.04	0.02
95	0.001	0.06	0.001	0.03	0.03	0.01	0.03	0.02	0.01	0.02	0.03	0.01	0.03
≥100	0.001	0.08	0.02	0.05	0.03	0.01	0.03	0.07	0.01	0.04	0.001	0.01	0.06

Table A1-4 Number of Striped Bass ≥30 cm TL measured by year in the upper Connecticut River during 1993-2004 (T. Savoy, unpublished data) and during 2006-07 (Davis et al. 2012; aggregated across 2006-07).

Year	n
1993	31
1994	62
1995	48
1996	148
1997	180
1998	184
1999	120
2000	253
2001	176
2002	317
2003	315
2004	289
2006-07	606

Table A1-5 Number of Striped Bass lavaged by 50-cm size class in 2005-07 (Davis et al. 2012; aggregated across years), estimated proportions of fish in each size class that consume 0,1,2 herring daily (Davis et al. 2012), and estimated angler catch of Striped Bass ≥30 cm TL in spring 2008 in upper CT River (Davis et al. 2011; estimates for creel survey reach expanded to estimate total catch for the upper Connecticut River).

Size Class (cm)	Lavaged	q_0	q_1	q_2	Y_i
30	22	0.0	0.0	0.0	3,686
35	64	0.97	0.03	0.0	3,818
40	95	0.97	0.03	0.0	5,662
45	89	0.92	0.08	0.0	3,160
50	64	0.92	0.08	0.0	1,054
55	56	0.97	0.03	0.0	263
60	44	0.98	0.02	0.0	1,054
65	41	0.83	0.14	0.03	526
70	41	0.93	0.06	0.01	1,054
75	28	0.76	0.17	0.07	791
80	21	0.69	0.3	0.01	132
85	19	0.85	0.15	0.0	395
90	12	0.75	0.25	0.0	132
95	15	0.83	0.17	0.0	0
≥100	31	0.90	0.05	0.05	0

Table A1-6 Estimated coastal abundance of Striped Bass (ASMFC 2015), and deterministic estimate of Striped Bass abundance in upper Connecticut River based on ratio of 2008 upper Connecticut River Striped Bass population estimate (Davis et al. 2012) to estimated Striped Bass coastal abundance in 2008 (ASMFC 2015).

Year	$SB_{Coastal}$	$SB_{CT\ RIver}$
1982	33,277,173	26,378
1983	57,636,345	45,686
1984	62,182,638	49,290
1985	64,276,397	50,950
1986	59,041,809	46,800

Table A1-6 (*continued*)

1987	69,122,769	54,791
1988	86,164,649	68,300
1989	98,913,839	78,406
1990	126,113,772	99,966
1991	121,356,630	96,195
1992	123,811,055	98,141
1993	146,854,794	116,407
1994	245,025,152	194,223
1995	212,323,850	168,302
1996	217,579,142	172,468
1997	249,831,085	198,033
1998	205,244,887	162,691
1999	195,706,557	155,130
2000	171,161,520	135,674
2001	200,199,733	158,692
2002	227,703,157	180,493
2003	175,685,650	139,260
2004	250,403,362	198,486
2005	198,404,830	157,269
2006	177,750,844	140,897
2007	148,172,323	117,451
2008	158,371,676	125,536
2009	133,320,676	105,679
2010	141,562,606	112,212
2011	162,718,344	128,981
2012	195,817,571	155,218
2013	114,485,056	90,749
2014	134,392,835	106,529